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Habitat, population structure and the conservation status of *Araucaria bidwillii* Hook. in the Australian Wet Tropics.

Thesis submitted by

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DECLARATION

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution. Information derived from the published or unpublished work of others is acknowledged throughout the text and in the references.

30 October 2015

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Signature Date

ABSTRACT

Araucaria bidwillii, commonly known as the bunya pine, is a widely recognised Australian conifer celebrated for its cultural, biogeographic and evolutionary significance. Belonging to the Araucariaceae, one of the oldest surviving families of trees, *A. bidwillii* is today found only in Far North and South East Queensland. This thesis provides the first quantified assessment of the habitat, population structure, abundance and conservation status of the Mount Lewis subpopulation of *A. bidwillii.*

My objective was to provide life history and ecological data in support of management planning and conservation practices that do not rely on assumption and anecdote. Prior to this study, the Mount Lewis subpopulation of *A. bidwillii* was thought to be restricted to approximately six discontinuous stands in two adjacent sub-catchments. With new occurrence records obtained from these catchments, a species distribution model was developed to identify potentially suitable habitat at both the local and regional scales. Rainfall, temperature and proximity to the rainforest boundary made significant contributions to the model's performance. With records from both tall open forest and rainforest included within the model, predicted habitat was often in alignment with the margin of these two vegetation types. Locally, predicted habitat aligned with known locations and identified other nearby sites with high habitat suitability values. However, the model failed to align with the other known Wet Tropics subpopulation approximately 100 km to the south in Wooroonooran National Park.

Population structure and recruitment patterns were investigated by establishing 13 study sites across tall open forest and rainforest. Size-class data, as a proxy for age, and individual counts of seedlings were obtained for *A. bidwillii* across these sites. The aggregated data for the entire sample population displays a reverse J-curve structure, often interpreted as an indication of continuous recruitment. However, further analysis identified variation in pattern in response to vegetation type. The results identify recruitment but there is no clear single strategy displayed. While there is an abundance of seedlings, there are very few subsequent size-classes and an almost constant low number of trees between 15cm DBH to approximately 100cm DBH. Interpretation of these results leads to some support for a temporal recruitment strategy interwoven with the vegetation dynamics of tall open forest and rainforest. Seedlings are abundant in tall open forest and in open rocky sites within rainforest. In well-developed rainforest seedlings are sparse and the population structure resembles a slight pulse or modal pattern. Beyond seedling establishment, persistence into reproductively mature size-classes is low overall.

The Mount Lewis subpopulation of *A. bidwillii* was identified as a genetically distinct and evolutionary significant unit in 2004. It is also isolated from other populations, is at the northern extremity of the taxon’s range and is exposed to unique threats not faced by subpopulations elsewhere. For these reasons, a conservation assessment of the Mount Lewis subpopulation was undertaken using the International Union for the Conservation of Nature criteria. Although within the protected area estate, the Mount Lewis subpopulation is considered ‘vulnerable’ due to a very restricted range, small number of mature trees, ongoing threats from fire, environmental weeds and the low likelihood a stochastic event will result in a population decline >50% over 100 years.

The northern subpopulation of *A. bidwillii* favours open sites over rainforest for seedling establishment. This finding is consistent with recruitment strategies of other *Araucaria* in South America, New Guinea and New Caledonia where vegetation dynamics influence population structures. At Mount Lewis the recruitment of *A. bidwillii* may be partly dependent on a long-term temporal interaction between tall open forest and rainforest. Beginning as a seedling in tall open forest and if able to escape the seedling bank, *A. bidwillii* may outlive surrounding eucalypts to eventually become a structural emergent in the subsequent rainforest over several hundred years.

Tall open forest is an important habitat for *A. bidwillii*, which may have implications for the ongoing use of fire as a management tool intended to restrict rainforest expansion. Ensuring the ecological processes that have allowed *A. bidwillii* to persist within the landscape can continue to operate is likely to be the most effective conservation strategy for this important subpopulation of a species of great significance.

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1. Introduction

Australia's Wet Tropics World Heritage Area is celebrated for its diversity of ancestral and ancient flora. Despite extensive research into the ecology of the region's rainforests, the gymnosperms have been relatively overlooked in favour of flowering plants.

This research provides some of the first ecological information of one of the region's most uncommon conifers, *Araucaria bidwillii* Hook. (Araucariaceae). Well known as the bunya pine, *A. bidwillii* is arguably Australia's most charismatic, celebrated and recognised conifer (Figure 1).

Figure 1. ***Araucaria bidwillii*** **growing on the margins of rainforest and tall open forest in Leichhardt Creek catchment, near Mount Lewis, in the Australian Wet Tropics World Heritage Area.**

1.1 The Araucariaceae

The Araucariaceae (Gymnosperma) is one of only three Australian families in the order Coniferales and is represented by three extant genera; *Agathis*, *Araucaria* and *Wollemia* (K. Hill, 1998; R. Hill & Brodribb, 1999). Amongst these three genera are 33 species including 13 *Agathis*, 19 *Araucaria* and one *Wollemia* (Enright et al., 1995; Setoguchi et al., 1998).

Although once globally widespread, the Araucariaceae are now largely found only in the southern hemisphere. The degree to which angiosperms caused the displacement of the Araucariaceae and other southern conifers remains unclear. In many habitats however, conifers posses physiological traits and display various recruitment strategies allowing them to co-occur with, or outcompete angiosperms (Bond, 1989; Brodribb et al., 2005; Brodribb et al., 2012).

The global decline of Araucariaceae is contrasted by their successful colonisation and adaptive radiation on more modern island geologies of the Asia Pacific. Spanning habitats from sub-alpine to tropical regions, current biogeography of Araucariaceae in the southern hemisphere is potentially a function of niche-based recruitment strategies such as those identified by Ogden et al. (1987), Enright et al. (1999) and Brodribb et al. (2012).

Queensland's Wet Tropics bioregion supports five of the six species of Araucariaceae found on mainland Australia, including *A. bidwillii.* All Australian Araucariaceae are restricted in distribution to the eastern coastal ranges of the Great Dividing Range (or associated coastal islands) with the exception of *A. heterophylla* found in Norfolk Island (K. Hill, 1998).

1.1.1 Evolution

Araucarian forests were once widespread in the northern and southern hemispheres with fossils dating back nearly 200 million years (Hernandez-Castillo & Stocky, 2002).

Araucarian plant parts including cones, cone scales and pollen have been retrieved from Europe, Asia, North America, Africa and Antarctica (Kershaw & McGlone, 1995; Setoguchi et al., 1998; Stocky, 1982). The Araucariaceae are now extinct in all of these places except for some minor occurrences in South East Asia.

Araucarian fossils can also be found throughout most of the present range of the family including South America, Australia and New Zealand (Stocky, 1982; White, 1998). Within Australia, fossils have be found in Tasmania, Western Australia, Victoria, New South Wales, and Queensland (Cantrill, 1992).

The phylogenetic relationship among extant Araucariaceae were explored in detail by Setoguchi et al. (1998) who conclude that their evolution began with the emergence of an ancestral taxon in Gondwana some time during the Mesozoic. Based on cpDNA *rbcL* sequence data, *Wollemia* is thought to have diverged first, followed by *Agathis* and then *Araucaria* (Biffin et al., 2010; Setoguchi et al., 1998).

Today's surviving *Araucaria* are divided into four sections: *Eutacta*, *Columbea*, *Intermedia* and *Bunya* (R. Hill & Scriven, 1998; Pye, 2005; Setoguchi et al., 1998; Stocky, 1982). Originally, the division was based on morphological characteristics but is also well supported by genetic sequencing (Setoguchi et al., 1998) and fits neatly into the current geographic distribution of *Araucaria* (Table 1).

Table 1. **Section Groupings of Extant *Araucaria*.**

Section	No. Extant Species	Distribution
Eutacta	15	New Caledonia (all 13 endemic species), Australia, Indonesia, Papua New Guinea (*A. cunninghamii*), Norfolk Island (*A. heterophylla*)
Columbea	2	Chile, Argentina, Brazil (*A. araucana, A. angustifolia*)
Intermedia	1	Papua New Guinea (*A. hunsteinii)*
Bunya	1	Australia (*A. bidwillii*)

Based on the fossil record, sections *Eutacta* and *Bunya* date to the Jurassic and represent the oldest lineages of extant *Araucaria* sections (Setoguchi et al., 1998; Stocky, 1982). Section *Bunya* is thought to have reached its widest distribution within the Mesozoic during the Jurassic approximately 145 million years ago (Hernandez-Castillo & Stocky, 2002). The extinct *Araucaria sphaerocarpa* from the Jurassic formations in England is anatomically similar to *A. bidwillii* and is placed within the *Bunya* section (Stocky, 1982). However, *A. bidwillii* has a closer relative from the Jurassic in Argentinean Patagonia; *Araucaria mirabilis* (Hernandez-Castillo & Stocky, 2002). The Cerro Cuadrado Petrified Forest, where *A. mirabilis* was found, has yielded a variety of fossilised tree parts including cones, scales, seeds and seedlings (Stocky, 1975).

Now the only remaining taxon in the *Bunya* section, *A. bidwillii* is restricted to regional refugia from which there is little prospect of any natural long-distance dispersal.

In contrast, both *Agathis* and the *Eutacta* section of *Araucaria* have expanded and diversified within the Asia Pacific region. Kershaw & Wagstaff (2001) point out that the geological environments, in which Araucariaceae has more recently evolved such as in New Caledonia, are not often conducive to the establishment of well-developed rainforest. The ancestral *Agathis* and *Araucaria* stock (of potential Australasian origin) is thought to have colonised new lands within the Asia Pacific region at a time when geological processes (tectonic and volcanic) are likely to have given the Araucariaceae a competitive advantage over competing angiosperms (Kershaw & Wagstaff, 2001).

1.1.2 Biogeography

The Araucariaceae were a significant element of the Gondwanan flora at least until the Cenozoic Era about 66 million years ago (Kershaw & Wagstaff, 2001). However the combined impact of geological upheaval, successive ice-ages, competition with modern flora and anthropogenic influences have diminished the world’s Araucarian forests to a fraction of their former extent (Kershaw & Wagstaff, 2001).

During the Jurassic there were Araucarian forests in what is now eastern, southern and western Australia (R. Hill et al., 2000). However, as Australia broke from Gondwana, the continent experienced periods of aridity and glaciation reducing the existing Araucarian and emerging angiosperm forests to refugia. Fossil evidence from Lynch’s Crater suggests that the Araucariaceae began a further decline about 130,000 years ago (Kershaw et al., 2007). This also coincides with an increase in eucalypts and an increase in fire in the Australian landscape (Kershaw & Wagstaff, 2001).

Throughout their present-day range within Australia, the Araucariaceae are associated with fire protected niches within rainforests and infrequently burnt margins with adjacent sclerophyll communities including tall open forest (Boland et al., 2006; Kershaw & Wagstaff, 2001).

While *A. cunninghamii* is found in both New Guinea and Australia, there are two varieties. *A. cunninghamii* var. *cunninghamii* is found from Cape York Peninsula and along the Great Dividing Range to the Macleay River in northern New South Wales and is the most widespread of the Araucariaceae. In contrast, *A. bidwillii* is restricted to the Wet Tropics and South East Queensland, two disjunct bioregions.

Much of the former habitat of *A. bidwillii* has been modified since European settlement. Clearing for agriculture, forestry, infrastructure including dams and fire has all had an impact on natural stands of *A. bidwillii* in South East Queensland. However in far North Queensland, the natural stands of *A. bidwillii* have remained largely undisturbed since European arrival. While logging occurred at Mount Lewis up until the late 1980s, no harvesting of *A. bidwillii* took place (P. Stanton pers. comm.).

1.1.3 Ecology

Many Araucariaceae, and particularly *Araucaria*, share a variety of traits and recruitment strategies that have enabled their establishment and persistence across various climates and habitats of the southern hemisphere. These shared traits and strategies are centred on an ability to exploit landscape level disturbances, and persist through long-term successional vegetation dynamics (Brodribb et al., 2012; Enright et al., 1999; Finckh & Paulsch, 1995; Jaffré et al., 2010; Ogden & Stewart, 1995; Rigg et al., 2010; Souza, 2007). In many respects, these characteristics are synonymous with the majority of southern hemisphere conifers (Brodribb et al., 2012).

Angiosperm radiation and diversification about 100 million years ago is thought to have pushed gymnosperms, particularly conifers, to marginal habitats (Lidgard & Crane, 1988). The widely held view that angiosperms possess superior physiological traits and can outcompete gymnosperms influenced some of the earliest accounts of Araucarian ecology. Womersley (1958) considered that competition from angiosperms was behind the lack of observed *Araucaria hunsteinii* seedlings in New Guinea’s forests. While similar views on *A. hunsteinii* were also expressed by Havel (1971) and Gray (1975), it was not until more comprehensive work by Enright (1982a, 1982b, 1982c) that a clearer picture emerged. Studying both *A. hunsteinii* and *A. cunninghamii*, Enright (1982c) noted that the former requires disturbance to regenerate in its preferred habitat of upland ridges and steep slopes. Alternatively, *A. cunninghamii* appeared capable of continuous recruitment (Enright, 1982c).

In South America, both *Araucaria araucana* and *Araucaria angustifolia* exploit disturbance opportunities for recruitment and can outlive competing angiosperms once established (Burns, 1993; Finckh & Paulsch, 1995; Souza, 2007; Veblen, 1982). Through the analysis of size-class data, *A. araucana* appears to have modal or unimodal recruitment patterns; a response to various disturbance events including wind-throw, volcanism and fire and competition with angiosperms (Veblen et al., 1995; Veblen & Stewart, 1982). Similarly, populations of *A. angustifolia* in Brazil, were also found to display a unimodal recruitment pattern using size-class data (Souza, 2007) and play a catalytic role in forest patch formation within grassland (Silva & Anand, 2011).

Ogden (1985) and Ahmed and Ogden (1987) provided the first analysis of data on recruitment cohorts for New Zealand's *Agathis australis* using size-class as a proxy for age. In seeking to address the disparity between climax and succession theory surrounding New Zealand's conifer-angiosperm forests, the temporal stand replacement model (discussed in more detail on pages 37-39) was developed to explain the modal or unimodal recruitment patterns of *Agathis australis,* now central in describing Araucarian recruitment theory (Ahmed & Ogden, 1987; Ogden, 1985; Ogden & Stewart, 1995; Ogden et al., 1987).

In New Caledonia, *Araucaria laubenfelsii* has been subject to comparative studies of stand demographics in both rainforest and maquis (Rigg et al., 1998; Rigg et al., 2010). Through the use of size-class data *A. laubenfelsii* displayed continuous recruitment in maquis and young forest but displayed limited recruitment in mature forest (Rigg et al., 1998). Ten year monitoring of permanent plots confirmed earlier findings, identifying *A. laubenfelsii* as a long-lived pioneer, facilitating the development of forest in maquis (Rigg et al., 2010). A similar result was obtained for *Agathis ovata* which was observed to be capable of continuous recruitment in maquis though reliant on disturbance in forest (Enright & Goldblum, 1998).

Enright, et al. (1999) synthesised Araucarian forest dynamics for species where data was available in the western Pacific. The authors used existing and new data collected for *Agathis australis*, *Araucaria laubenfelsii* and *A. hunsteinii* to test the validity of Ogden's (1985) temporal stand replacement model. Using a variety of methods evidence was found in support of the model. Evidence included large recruitment cohorts, low rates of recruitment in mature stands and the need for open canopy requirements for each species for successful recruitment (Enright et al., 1999).

Although second only to New Caledonia in diversity of Araucariaceae, relatively little ecological research has been published on the six mainland Australian species. With the exception of Smith and Butler (2009) who found that the taxon is capable of dispersal and establishment in regenerating forests, very little has been published on the ecology of *A. bidwillii,* an observation made by Enright (1995).

Within the Wet Tropics, *A. bidwillii* has a very limited distribution and is confined to two localised and disjunct occurrences. Genetically distinct from its South East Queensland counterparts (Pye and Gadek, 2004), the Mount Lewis population in the northern Wet Tropics bioregion is the focus of this study.

1.2 *Araucaria bidwillii*

A. bidwillii was described in 1843 by WJ Hooker based on samples and notes sent to him by JT Bidwill (Blake, 2002). It is widely recognised throughout Australia as the bunya pine. Other common names include bunya bunya, bunya nut, or just bunya (Boland et al., 2006) which are English interpretations of Indigenous language names (Huth, 2002).

Endemic to Queensland, *A. bidwillii* is a large forest tree of outstanding evolutionary, biogeographic, conservation and cultural significance (Haebich, 2002; Jerome, 2002; Pye & Gadek, 2004; Tindale, 1974). Widely planted throughout Australia for its distinctive growth habit and edible nuts, *A. bidwillii* is a much-celebrated aspect of our national flora. *A. bidwillii* is listed by the IUCN as Least Concern (Thomas, 2011).

1.2.1 Species Description

Typically, *A. bidwillii* is a forest emergent often observed growing between 30 and 45m in height (Boland et al., 2006) but is capable of reaching approximately 50m at some sites (authors obs.) and occasionally exceeding 60m (Stanton et al., 2013). Predominantly, this species grows with a single, straight and barely tapered cylindrical bole (Figure 2). From near the often dome-shaped crown, whorled branches radiate out, often unbranched with foliage clustered at the ends (Boland et al., 2006; Hyland et al., 2003). A secondary or reiterated canopy may develop in trees exposed to greater light (Boland et al., 2006) (Figure 2).

Figure 2. ***A. bidwillii* growth habit in Leichhardt Creek catchment.**
Left: illustrates both a dome shaped canopy and a secondary, reiterated canopy due to light exposure. **Right:** *A. bidwillii* in well-developed Simple Notophyll Vine Forest with a conspicuous large strait bole only slightly tapered.

Leaves are sessile, variable in size from 5 to 25 mm and spirally arranged on branchlets (Hyland et al., 2003). Pye (2005) and Smith and Butler (2009) both report slight morphological differences in the acuteness of the leaf tip between the Wet Tropics and South East Queensland populations. Seedlings and juveniles produce a broader horizontal leaf, presumably to capture more light (Figure 3).

Monoecious, *A. bidwillii* produces male and female cones on a single tree. Female cones develop in the apex of the tree and can be up to 30 cm long and 20 cm wide (Boland et al., 2006; K. Hill, 1998). Seeds up to 5cm long are embedded within cone scales until maturity (Hyland et al., 2003), although cones are produced every year, there are mass fruiting events, masting, every three to four years (Smith & Butler, 2002).

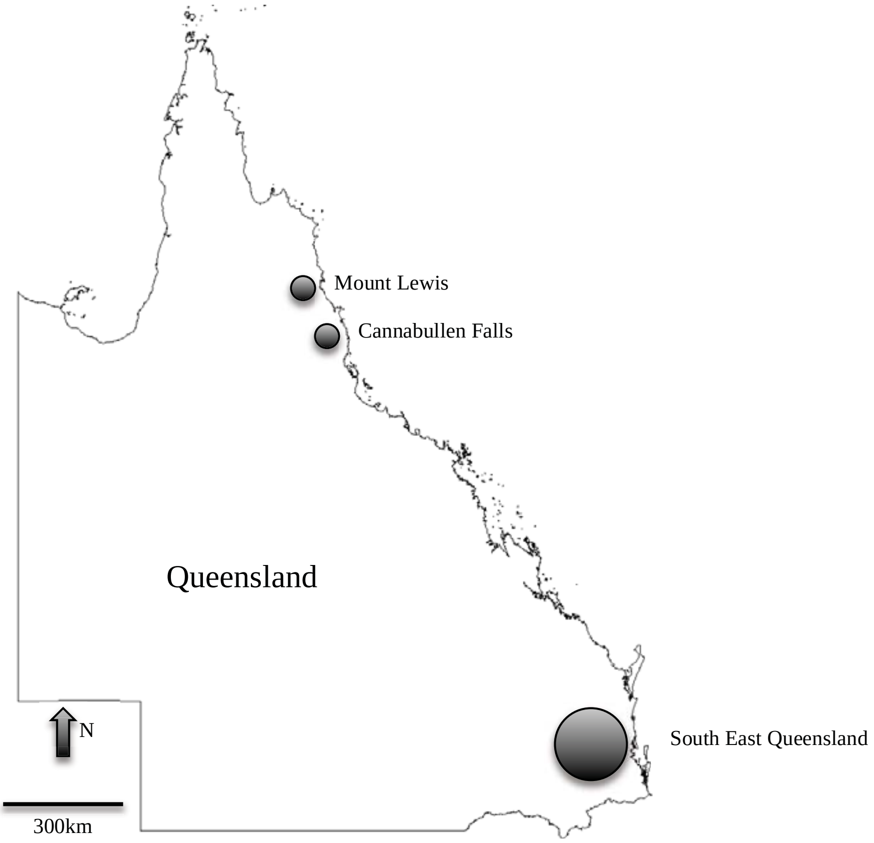
Dispersal of *A. bidwillii* seed has not been studied but it is thought gravity, water and occasional caching by mammals may play a role (author's obs.; Pye, 2005; Smith & Butler 2009). Predation of seed by cockatoos and rodents has also been observed and may lead to dispersal (author's obs.). Cryptogeal germination of *A. bidwillii* seed is facilitated by a thick taproot drawing the seed beneath the soil surface before the first leaves emerge (Burrows & Stockey, 1994).

Figure 3. ***A. bidwillii* growth habit in Leichhardt Creek catchment, juvenile foliage & sapling stem.**

Left: illustrates a young plant with broad horizontal foliage typical of seedlings and shade foliage on older trees. **Right:** shows a series of nodes where previous sets of whorled branches have occurred on a sapling that is *ca.* 3m tall but may be well over ten years old.

1.2.2 Species Distribution

The taxon is naturally found within South East Queensland and the Wet Tropics, two geographically disjunct Queensland bioregions (Boland et al., 2006; K. Hill, 1998). The limited distribution of *A. bidwillii* is thought to be a symptom of pre-historic reductions in range due to climatic changes and the taxon's inability to disperse over long distances (Smith & Butler, 2009).



Distribution Map: Indicative only, the above map illustrates the two Wet Tropics populations of *A. bidwillii* at Mt Lewis and Cannabullen Falls relative to the populations found in South East Queensland.

In South East Queensland *A. bidwillii* occurs from the Bunya Mountains in the west, through the Conondale Ranges to Gympie in the north (Boland et al., 2006). There are also recent records from the Sunshine Coast north of Brisbane (Smith & Butler, 2009).

Within the Wet Tropics bioregion, there are two subpopulations of *A. bidwillii*. At the northern extremity of the species range near Mount Lewis, six discrete stands within two adjacent sub-catchments occur on leasehold land managed by the Australian

Wildlife Conservancy. This has constituted the known extent of the Mount Lewis subpopulation. At Cannabullen Falls near Ravenshoe, a single stand is all that is known from Wooroonooran National Park. Preliminary fieldwork at Mount Lewis for this this project located mature *A. bidwillii* outside of the known stands, raising the potential that the subpopulation is more widespread.

Genetic research on *A. bidwillii* by Pye (2005) identified significant variation between the South East Queensland and Wet Tropics populations using random amplified DNA (RAPD) markers. This is illustrated in Pye's (2005) thesis with an unrooted UPGMA (unweighted pair group method with an arithmetic mean) tree (Figure 4) that places the Mount Lewis population on a long branch away from the South East Queensland populations. Both morphological and genetic differences, perhaps compounded by the different climatic conditions experienced by the two populations, suggest evolutionary divergence is currently operating within *A. bidwillii* (Pye & Gadek, 2004).

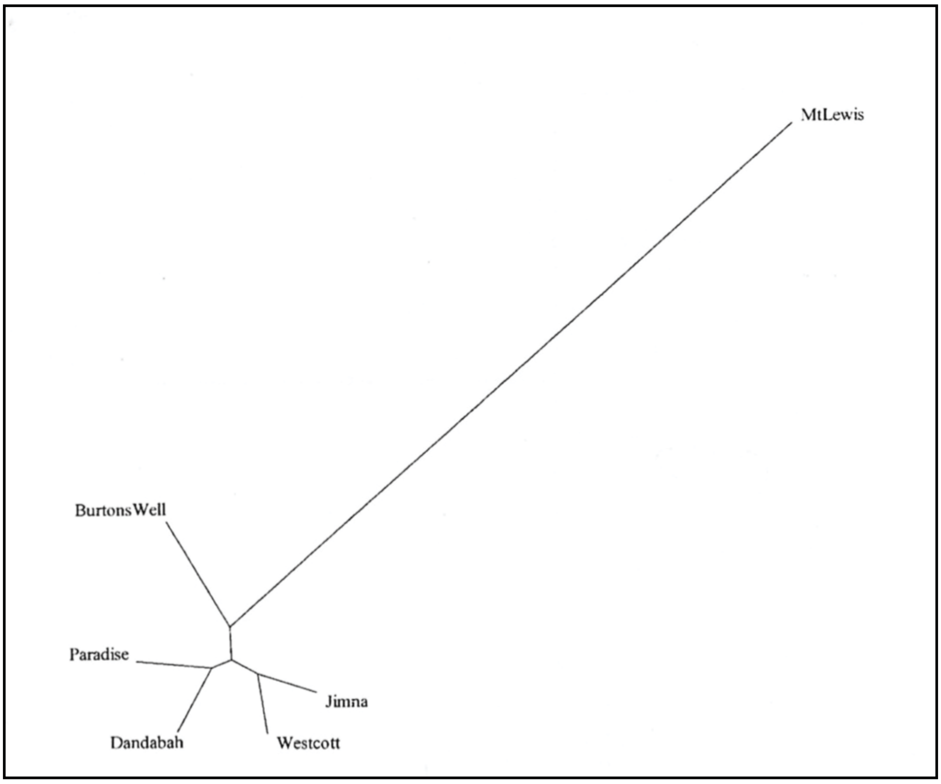


Figure 4. **UPGMA Tree displaying divergence within *A. bidwillii* populations.** Reproduced from Pye (2005) the above diagram displays the relative genetic divergence of sampled populations. In the left-hand corner, Burtons Well, Paradise, Dandabah, Westcott and Jimna represent South East Queensland populations with Mt Lewis on a long branch relative to its divergence.

1.3 Study Area

The known occurrences of the northern most subpopulation of *A. bidwillii* are restricted to two adjacent catchments on the western escarpment of the southern extent of the Carbine Tableland. Land tenure is mixed, with most of the Carbine Tableland within Daintree National Park while the southern and western areas are in Mount Lewis National Park. Some sections of the western draining catchments of the Carbine Tableland are leasehold or freehold land. The study area is within the Wet Tropics World Heritage Area, on Brooklyn Sanctuary leased and managed by the Australian Wildlife Conservancy (Figure 5). The closest towns are Mount Molloy and Julatten with Mareeba further south. Access to the known populations of *A. bidwillii* is via the Mount Lewis Road, which crosses Leichhardt Creek at about 900 metres altitude near the Australian Wildlife Conservancy's trailhead.

Fieldwork for this project was undertaken primarily in Leichhardt Creek catchment associated with Mount Lewis. A small amount of data was also collected from Station Creek, immediately south of Leichhardt Creek.

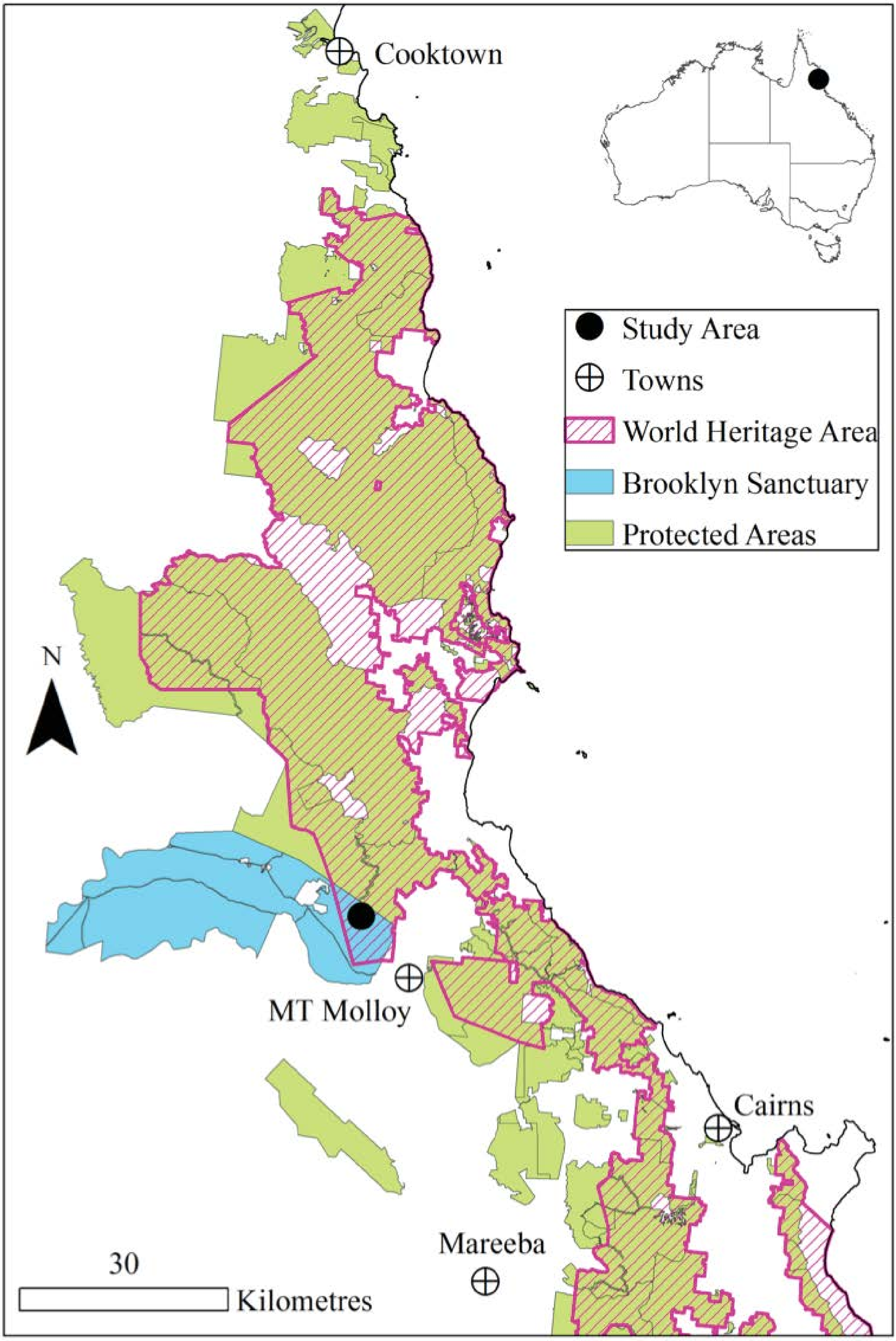


Figure 5. The study area relative to to the surrounding protected area estate, Wet Tropics World Heritage area and Australian Wildlife Conservancy's Brooklyn Sanctuary.

1.3.1 Mount Lewis

The Mount Lewis summit 1224m above sea level (asl.), is in the north east of Leichhardt Creek catchment and the predominant geology is composed of fine grained biotite granites (Nix, 1991). Mount Lewis is one of the highest summits on the Carbine Tableland together with nearby Mount Spurgeon at 1341m asl. Leichhardt Creek drains southwest of the Mount Lewis summit until it meets Mary Creek just before its confluence with the Mitchell River at approximately 350m asl. Over 1600 mm of rain falls across the Carbine Tableland while the summit regions receive in excess of 2000 mm and the wettest areas receive up to 3000 mm (Nix, 1991).

Apart from supporting the main known occurrences of *A. bidwillii* in the Wet Tropics, Leichhardt Creek catchment (Figure 6 & 14) was chosen as the main study area because of its accessibility and relatively navigable terrain. Some data was collected from the adjacent Station Creek. Leichhardt Creek also yielded more occurrences of *A. bidwillii* in a pilot study for this project than anticipated, particularly in tall open forest.

Within Leichhardt Creek catchment, two broad vegetation groups (BVGs) are of primary interest and were targeted during sampling for this project. This included tall open forest and closed rainforest. These two BVGs are discussed in more detail in the following section.

1.3.2 Vegetation and Habitat

At the higher altitudes between 900m to just over 1000m asl., the study area is dominated by upland rainforest. Depending on aspect, this gives way to tall open forest between 900m down to about 600m asl. Again, aspect and also geology then influence the occurrence of savanna vegetation. This is captured in the below (Figure 6) aerial image of Leichhardt Creek catchment with the higher altitude rainforest occurring on the right (east) grading into tall open forest along the escarpment ridges and mid catchment through to open savanna on the left (west).

Figure 6. **Aerial image of Leichhardt Creek catchment from over 1000m to 350m asl.**

The aerial image above illustrates the gradient from rainforest (brighter green on right of image) in the east at over 1000m asl. through tall open forest (darker green) that occurs along the escarpment before grading into savanna (indicated by the lighter green and brown on the left of the image) to the west. Leichhardt Creek flows north-west following the valley system through the image centre.

Vegetation classification used in this study is largely consistent (see below) with the Queensland Government’s broad vegetation groups (BVGs) (Neldner et al., 2015), regional ecosystem descriptions and earlier descriptive summaries.

BVGs are a high-level classification system that captures the dominant structure such as rainforest scrub, open forest or woodland and groups a number of different expressions under the one description depending on the scale unit (1:5 – 1:1 million). The two BVGs relevant to this study are rainforest and wet eucalypt open forest (herein referred to as tall open forest).

Within the study area, rainforest and tall open forest meet and interact over broad areas. At some sites this is characterised by a diverse mix of species of mature trees usually attributed to either rainforest or tall open forest. Often, *A. bidwillii* is present and competes for canopy space with the dominant species from either BVG. These environments, where there is an overlapping gradient between two communities, are broadly referred to as the ecotone (Hufkens et al., 2008). Ecotone is both a generic term used in ecology and also a regionally specific term used to describe associations of tall open forest and rainforest in North Queensland (Turton & Sexton, 1996).

Each of the two BVGs are described below with specific reference to their Queensland Government Regional Ecosystem classification. These are largely synonymous with their BVGs except for some slight but important local variation.

Rainforest

Rainforest within the study area (Figure 7, left) is synonymous with Tracy's (1982) Type 8 simple notophyll vine forest the Queensland Government's BVG1M: 6b and regional ecosystem 7.12.16c. Within the study area, rainforest typically has a canopy height of around 30m, occasionally with emergent *A. bidwillii* rarely exceeding 40m and occurs at altitudes ranging from over 900m to about 700m. Dominant canopy trees include *Podocarpus grayae* de Laub. (Podocarpaceae), *Flindersia* spp., *Garcinia* spp., *Elaeocarpus* spp., *Syzygium* spp., *Ficus* spp., and species from Proteaceae, Sapindaceae, Cunoniaceae, Myrtaceae and Lauraceae.

Understory is variable in density, includes various *Alpinia* spp., *Aglaia tomentose* Teijsm. & Binn. (Meliaceae), *Ardisia brevipedata* Muell. (Myrsinaceae), *Calanthe triplicata* Ames. (Orchidaceae), *Calamus* spp., *Smilax glyciphylla* Sm. (Smilaceae) and a variety of ferns where light is more abundant. Local variation includes rocky sites where the rainforest canopy is less well-developed, often giving rise to a greater abundance of *A. bidwillii* (author's obs.).

Simple notophyll vine forest is of least concern under Queensland's *Vegetation Management Act 1999* with >30% of pre-clearing area remaining. Current management practice is to protect this community from fire through the deliberate burning of surrounding 'fire adapted' ecosystems (Queensland Government, 2014).

Tall Open Forest

Tall open forest within the study area (Figure 7, right) is typical of Type 14a (Tracey 1982), BVG1M: 8a and regional ecosystem 7.3.42. It is characterised by mature and senescent *Eucalyptus grandis* W.Hill (Myrtaceae) with a mixed understorey of open forest and rainforest species. Some areas within Leichhardt Creek are also relatively open and consistent with Regional Ecosystem 7.12.21, which has an understorey of open forest species.

In addition to *E. grandis,* this BVG is also characterised by the presence of *Syncarpia glomulifera* subsp. *glomulifera* (Myrtaceae), *Allocasuarina torulosa* Aiton (Casuarinaceae), and occasionally *Banksia aquilonia* A.S.George (Proteaceae). In a limited number of sites *A. bidwillii* is present as a mature canopy tree amongst *E. grandis.*

The understory includes a mix of pioneer rainforest species including *Polyscias australiana* Muell. (Araliaceae), *Dendrocnide moroides* (Urticaceae), *Eupomatia laurina* R.Br. (Eupomatiaceae) and a range of longer-lived canopy species. *Calamus* spp. and *Alpinia* spp. are abundant in the understorey as are numerous grasses in lighter patches.

Similar to the rainforest BVG, a greater abundance of site rockiness supports a greater density of *A. bidwillii* (author’s obs.).

Regional ecosystem 7.3.42 is ‘of concern’ under Queensland’s *Vegetation Management Act 1992* and has an endangered status within the Wet Tropics bioregion. Current management practice includes prescribed burning on a rotation between 3 and 10 years depending on the understory type expected or desired. Burning allegedly controls an ‘overabundance’ of rainforest tree recruitment in the mid-stratum (Queensland Government, 2014).

Regional ecosystem sub-unit 7.3.42b has a well-developed rainforest understory which is common within Leichhardt Creek. Most occurrences of *A. bidwillii* from within the tall open forest BVG recorded in this study are from this regional ecosystem sub-unit, which is characterised by a complex understory of rainforest species.

Some authors and land managers suggest eucalypt forest is being replaced by rainforest (Hopkins et al., 1996; Unwin, 1986) and recommend intervention through the use of fire on short rotations (Harrington et al., 2000). However, Tng et al. (2011) identified that most rainforest boundaries have remained stable over the last 50 years and expansion is much slower than previous estimates. It is unclear what impact contemporary management inventions, such as the use of fire, will have on the long-term recruitment processes of *A. bidwillii* in ecotone environments.

Figure 7. **Habitat of *A. bidwillii* in Leichhardt Creek catchment.**
Left: mature *A. bidwillii* is widely dispersed in rainforest within the catchment.
Right: mature *E. grandis* and *A. bidwillii* occasionally co-occur in tall open forest.

1.4 Aims and Objectives

This research attempts to answer three questions about the distribution, recruitment and conservation status of the Mount Lewis subpopulation of *A. bidwillii*. In doing so, this research will test assumptions and present new information on the ecology of the northern most subpopulation of *A. bidwillii*.

The first aim of this project is to predict the likely distribution of the Mount Lewis subpopulation of *A. bidwillii* within adjacent sub-catchments along the western escarpment of the Carbine Tableland by answering the following question:

1. *Can climatic and environmental variables predict potentially suitable habitat and the likely distribution for the Mount Lewis subpopulation of A. bidwillii?*

The second aim is to investigate the population structure and potential recruitment patterns of the Mount Lewis subpopulation of *A. bidwillii* across its habitat. While anecdotal observations of recruitment exist, the population structure has not been previously examined which is an important step in documenting recruitment. This aim will be met by answering the following question:

2. *Does the Mount Lewis subpopulation of A. bidwillii display evidence of continuous recruitment within its population structure?*

The third aim is to establish the Mount Lewis sub-population of *A. bidwillii* as a conservation and management priority by using the International Union for the Conservation of Nature (IUCN) categories and criteria. This aim will be met by answering he following question:

3. *What is the conservation status of the Mount Lewis subpopulation of A. bidwillii?*

Combined, these research aims will enable an informed assessment of the conservation status of the Mount Lewis subpopulation of *A. bidwillii* identifying management priorities and assist in conservation planning.

1.5 Research Approach

The preceding sections in Chapter 1 articulate the importance of this study, outlining the evolutionary, biogeographic and conservation significance of the Araucariaceae and *A. bidwillii.* Detail is also provided on Mount Lewis, the vegetation and habitats of the study area and identifies knowledge gaps and potential threats.

Chapter 2 addresses the first aim through the use of a species distribution model performed using Maxent (Phillips et al., 2006). Sample sites (for Chapter 2) and incidental records for *A. bidwillii* from Mount Lewis area are used to generate geospatial habitat modelling and mapping.

To address the second of the above aims, Chapter 3 explores the population structure of *A. bidwillii* through the collection of size-class data as a proxy for age. Although there are some limitations with this approach, it enables valid comparisons to be made between habitats on the abundance and density of *A. bidwillii.*

In Chapter 4 I investigate the conservation status of the Mount Lewis subpopulation of *A. bidwillii.* With the data obtained from Chapters 2 and 3 I am able to make informed inferences on specific IUCN criteria (IUCN Red List Committee, 2013) used to assess the conservation status of species, subspecies or varieties. In this exercise I treat the Mount Lewis subpopulation of *A. bidwillii* as a distinct management unit.

Conclusions drawn from the results and discussion of Chapters 2, 3 and 4 are presented in Chapter 5 together with recommendations.

2. Distribution Modelling

Current Queensland Government vegetation mapping identifies six discrete locations where *A. bidwillii* occurs near Mount Lewis. While these locations are relatively accurate and were essential in the design of this research, it was established during a pilot study I undertook for this research that *A. bidwillii* occupies a much greater area and is not restricted to rainforest as previously assumed. As a subpopulation of conservation interest and at the northern edge of its range, I have used available data and existing methodologies to identify the extent of potentially suitable habitat.

The primary aim of this chapter is to predict the potential distribution of habitat for the Mount Lewis subpopulation of *A. bidwillii* along the western escarpment of the Carbine Tableland near Mount Lewis, in the Australian Wet Tropics region by answering the following question:

Can climatic and environmental variables predict potentially suitable habitat and the likely distribution for the Mount Lewis subpopulation of A. bidwillii?

A secondary aim is to predict potentially suitable habitat throughout the Wet Tropics based on the Mount Lewis occurrence records to identify if there is any consistency with the only other known location in the Wet Tropics at Cannabullen Falls, approximately 65 kilometres to the south.

2.1 Introduction

Predicting the potential distribution of a species by understanding its relationship with climatic and environmental variables can deliver multiple ecological, management and conservation outcomes (Elith et al., 2011; Franklin, 2010; Phillips et al., 2006). Quantifying the influence of environmental attributes on the occurrence of species first began as early as 1807 with climate, later including other environmental attributes by the mid 20th century (Guisan & Thuiller, 2005; Guisan & Zimmermann, 2000). Known as species distribution modelling (SDM), it wasn't until the 1970s that significant advances were made in this field of ecology. Since this time it has become increasingly invaluable to ecological practitioners and conservation planners (Zimmermann et al., 2010).

Today, SDMs are used to establish statistical inferences about the relationship a taxon has with its surrounding environmental conditions across its range. This approach is central to predictive geo-spatial modelling and invaluable in the planning and management of species and communities of conservation significance (Franklin, 2010; Guisan & Zimmermann, 2000; Wiersma et al., 2011; Zimmermann et al., 2010).

Predictive modelling relies on testing the influence of a range of environmental variables including climatic, biotic and abiotic factors on the distribution of a species or community (Franklin, 2010). Information derived from such modelling is important for identifying potential habitat for species of interest. This can include historical, contemporary or future predictions depending on the purpose of the modelling task (Elith et al., 2011; Tittensor et al., 2009; VanDerWal, Shoo, Johnson, et al., 2009).

Beginning with observations of a species' occurrence, presence only SDMs are developed through the analysis of the environmental variables associated with these occurrences using statistically based or rule-based approaches (Franklin, 2010; Phillips et al., 2006). This is typically referred to as niche-based or habitat suitability modelling.

Within the Australian Wet Tropics, predictive modelling has been used to investigate both the distribution of species and predicted shifts of species' in response to historical and projected climate change (Costion et al., 2015; Graham et al., 2010; VanDerWal, Shoo, Johnson, et al., 2009; VanDerWal, Shoo, & Williams, 2009).

Using presence-only data requires an awareness of the general ecology of the species of interest, the quality of data and potential bias. This includes an understanding of the species' dispersal mechanisms, landscape barriers that would influence distribution not captured in spatial data and contemporary landscape disturbances rendering otherwise suitable sites unsuitable (Elith et al., 2011; Phillips et al., 2006).

Following the modelling analysis, suitable conditions are mapped in geographic space, effectively identifying the fundamental niche (Phillips & Dudik, 2008). The realised niche, as opposed to the fundamental niche, is where the modelled species actually occurs. In interpreting the fundamental and realised niche it is important to consider barriers to distribution and dispersal ability, the latter particularly relevant to *A. bidwillii* which has very limited dispersal potential.

A popular and widely used approach in SDM is the maximum entropy (Maxent) technique (Phillips et al., 2006). Used extensively since becoming available in 2004, Maxent works by using presence-only data and a set of environmental variables for the study area (Elith et al., 2011; Phillips et al., 2006). While used in increasingly complex analyses, Maxent can be used for simple exploratory analysis of data to produce predictive maps of habitat suitability and corresponding habitat suitability values on a scale from 0 to 1 (Merow et al., 2013; Phillips et al., 2006).

Central to Maxent analysis is an estimate of the ratio of the suitability of one place versus another that relies on covariate data (Elith et al., 2011). It does this by weighting all of the original observations evenly then performs an optimisation routine iteratively improving the fit of the model.

2.2 Methods

2.2.1 Study Area

The study area comprises the Australian Wet Tropics region. In addition, approximately 84 square kilometres of the Wet Tropics associated with the western escarpment of the Carbine Tableland near the summits of Mount Lewis and Mount Fraser are an area of specific focus.

2.2.2 Occurrence Data

A total of 97 mature trees (unique occurrence records) for *A. bidwillii* were obtained for this study (Figure 8). These records were made during extensive fieldwork in Leichhardt Creek catchment from 2008 through to 2012 with a small number of additional records obtained from the adjacent Station Creek catchment in 2010.

Survey effort and approach was based on locating the 13 study sites for Chapter 2 with the aim of achieving a diversity of aspect, vegetation and location through stratified random sampling. All 97 records were for reproductively mature specimens of *A. bidwillii.*

From 2008 to 2010, data was captured on a Garmin GPS 60. From 2010 onwards data was captured on a Garmin Oregon 300 in GDA94 format. The latter device has a greater accuracy while the former may have been inaccurate by up to 14 metres in some locations. Survey tracks and walking routes were also recorded.

Point data was downloaded into Garmin BaseCamp software (version 4.2.2.0), exported as CSV files and converted into metres format to match the spatial data set for the Wet Tropics.

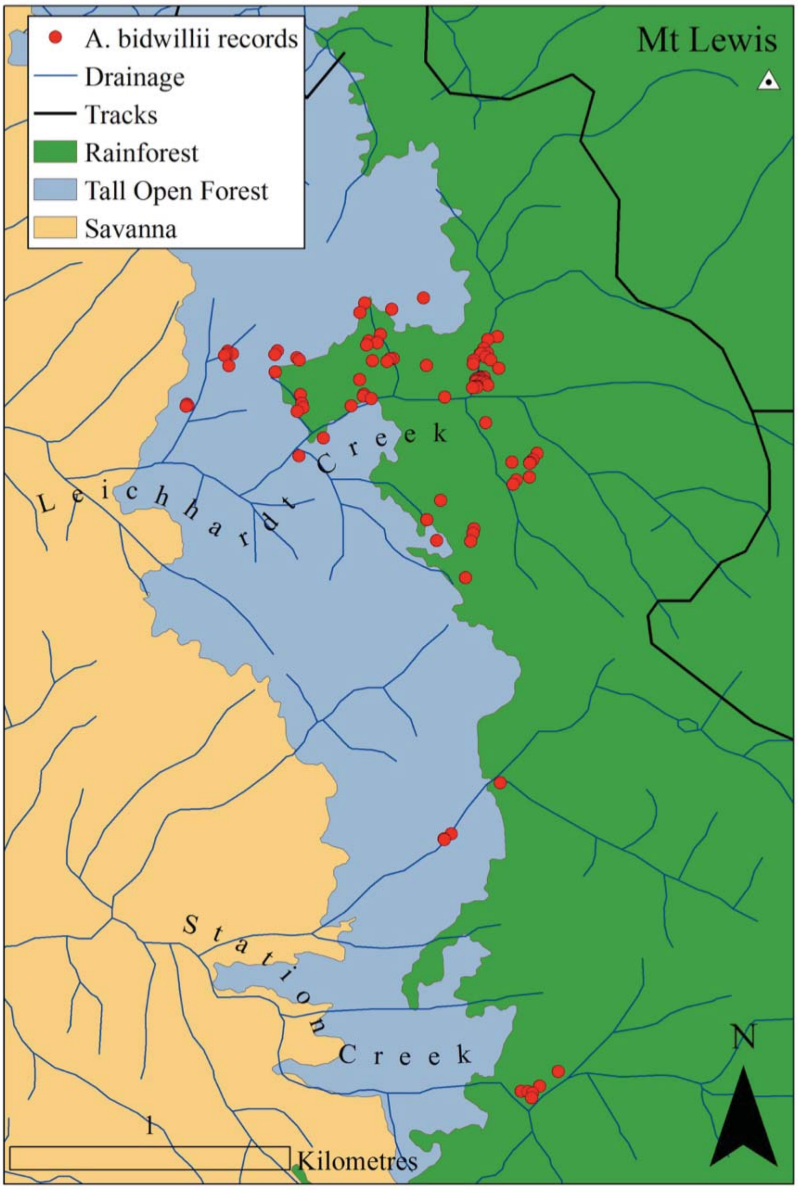


Figure 8. **Recorded locations of the Mount Lewis subpopulation of *A. bidwillii* used in the SDM from Leichhardt and Station Creeks and the broad vegetation groups.**

2.2.3 Environmental Data

The Wet Tropics study area used for this exercise of species distribution modelling was consistent with previous studies and included a 20 km buffer of surrounding environments to capture a broader area (Costion et al., 2015; Graham et al., 2010; VanDerWal, Shoo, Johnson, et al., 2009).

An 80-metre geospatial raster grid was created for the study area using Arc GIS software. Each grid cell contained information of each of the environmental variables described below. A total of 5,722,571 grid cells were spread across the site 3,662,446 hectare region.

Spatial environmental data was obtained for the study area including aspect, geology, rainfall, slope, temperature, vegetation and soil. Distance to rainforest edge and drainage were also calculated and included. Each variable was clipped to fit the same 80 metre grid.

Consistent with the underlying grid, topographic variables were derived from an 80 metre grid Digital Elevation Model (Accad, 1999; Rochester, 2003), including slope and aspect.

Geology and soil were derived from the Australian Soil Research Information System's (http://www.asris.csiro.au/) (ASRIS) mapped soil data at a scale of 1:2,000,000.

Climatic information was obtained from spatially interpolated climate data via ANUCLIM Version 6.1 (Xu & Hutchinson, undated).

Vegetation types used in this study are based on the Queensland Broad Vegetation Groups (Neldner et al., 2015) and includes simple evergreen notophyll vine forests (rainforest) wet eucalypt tall open forest (tall open forest) and savanna which are the basis of Queensland's regional ecosystem mapping.

2.2.4 Modelling Protocol

Maxent version 3.3.3, was used to model potential habitat for *A. bidwillii* within the Australian Wet Tropics region under current climatic and environmental scenarios.

Maxent was chosen for its straightforward user interface, availability, performance and wide use in the Wet Tropics region.

Following the identification of categorical data, basic settings were adjusted. The random test percentage was set at 25, the standard random 10,000 background points were retained, with 15 replicates (providing an average of each model run) and cross-validation selected. In advanced settings, maximum iterations were set at 5000. The option to do a jack-knife measure of variable importance was also selected.

Of the 97 occurrence records available, 38 were used as training samples and 12 were used as testing samples. The Maxent software automatically excluded the remaining 47 occurrence records because they were duplicate occurrences within the 80 metre geospatial raster grids.

Model performance and evaluation was measured by the “area under the curve” (AUC) statistic. AUC values from 0.5-0.7 are low accuracy, 0.7-0.9 are medium accuracy and considered useful, while >0.9 is regarded to be highly accurate (Franklin, 2010; Swets, 1988).

Habitat suitability values (HSV), scores between 0 and 1, are the primary tool used in the geospatial projection of the mapping output from the Maxent model.

2.2.5 Limitations

Limitations and potential pit-falls can impede the production of a meaningful result or model using Maxent (Phillips et al., 2006).

One problem is drawing samples from too small an area and sampling bias. Too small a sampling area and reliance on more easily accessible localities can lead to spatial auto-correlation. The model output risks being a reflection of the survey effort where species records are influenced by sampling bias (Elith et al., 2011).

However, *A. bidwillii* was not observed along any road or old forestry track within the area. All stands and emergent mature trees are only accessible on foot with the average distance of the thirteen study sites 1.2 kilometres from the Mount Lewis Road.

2.3 Results

The Maxent modelling algorithm, using 9 environmental variables, identified a patchy and narrow ecological niche for *A. bidwillii* within the Australian Wet Tropics region. The average test AUC was 0.997 (±0.001) with the most important variables being rainfall (29.9%) distance to rainforest (29.8%) and temperature (33.9%) permutation importance (Table 2, Appendix 1).

Table 2. Relative contributions of environmental variables to model.

Variable	% Contribution	Permutation Importance (%)
Geology	22.9	3.7
Rainfall	19.2	29.9
Distance to Rainforest Boundary	19.1	29.8
Temperature	16.7	33.9
Aspect	8.2	0.5
Soil	3.4	1
Vegetation Type	7.5	0.1
Slope	2.1	0.1
Distance to Drainage	0.9	0.9

The jack-knife measures of variable importance also revealed the climatic variables of rainfall and temperature have the most influence on the model. This was consistent with the training and test gain and AUC jack-knife tests. Vegetation type was also third highest in the AUC jack-knife test behind rainfall and temperature.

2.3.1 Wet Tropics

For the Australian Wet Tropics region the predicted ecological niche, or potential habitat, was scattered in isolated locations from the Windsor Tableland in the north to the Paluma Range in the south (Figure 9).

Most of the predicted ecological niche has a low HSV between 0.22 – 0.33 out of a scale between 0 – 1. Very few locations had a habitat suitability value greater than 0.67.

Many of the predicted areas of potentially suitable habitat are inland and often on the western fall of various ranges.

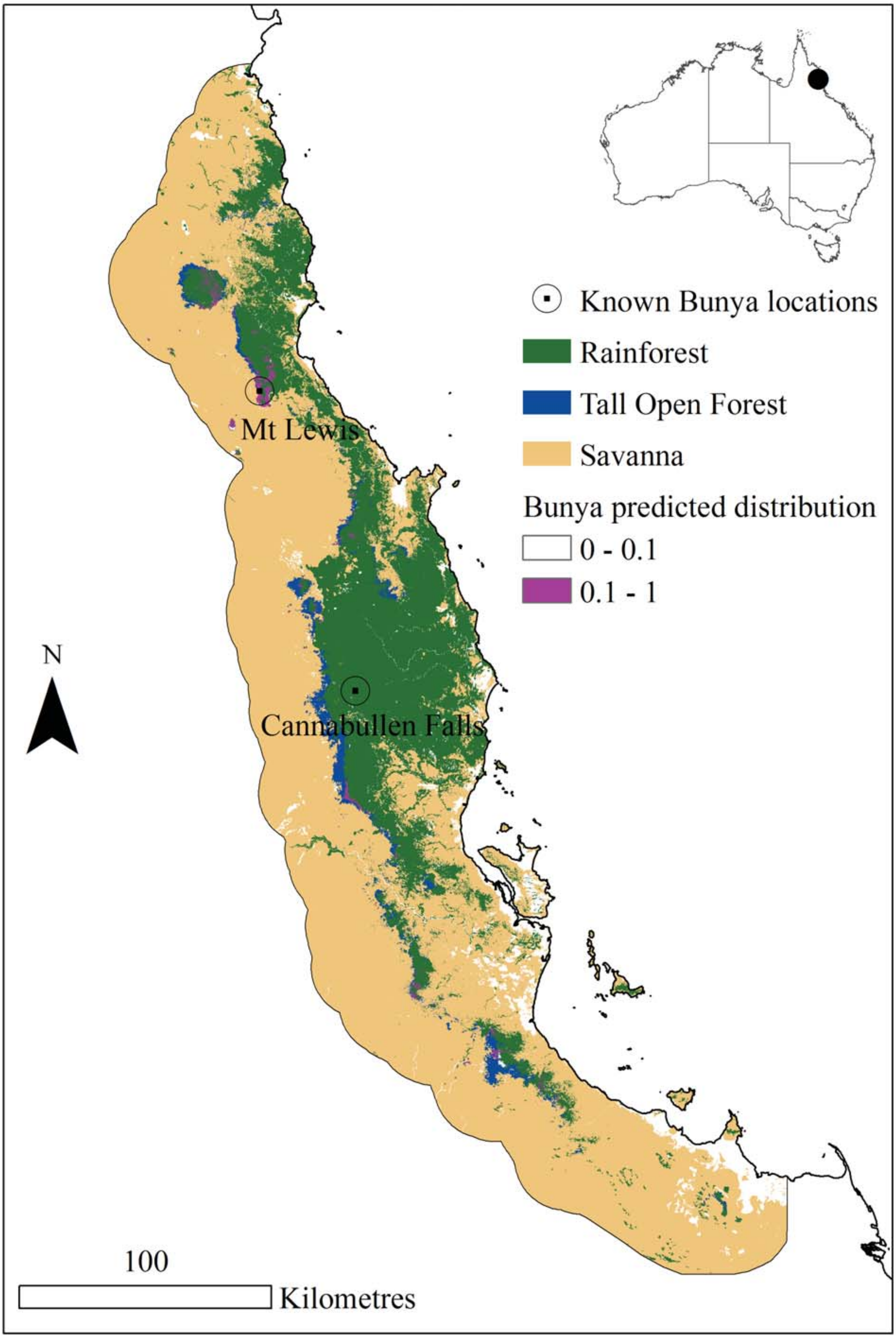
A small mountain known as Bakers Blue, 22km southwest of Mount Lewis possesses areas with habitat suitability values between 0.56 – 0.78. This is considered in more detail in the discussion section.

This model failed to predict the known population of *A. bidwillii* at Cannabullen Falls in Wooroonooran National Park, providing a habitat suitability value of 0 for that location (Figure 9).

In Figure 9, the HSV values have been grouped into everything over 0.1 due to the mapping scale and the intention of this map to illustrate predicted distribution and the two known localities in the region.

Figure 9. **Predicted distribution of *A. bidwillii* for the Australian Wet Tropics region with grouped HSV values and BVGs.**

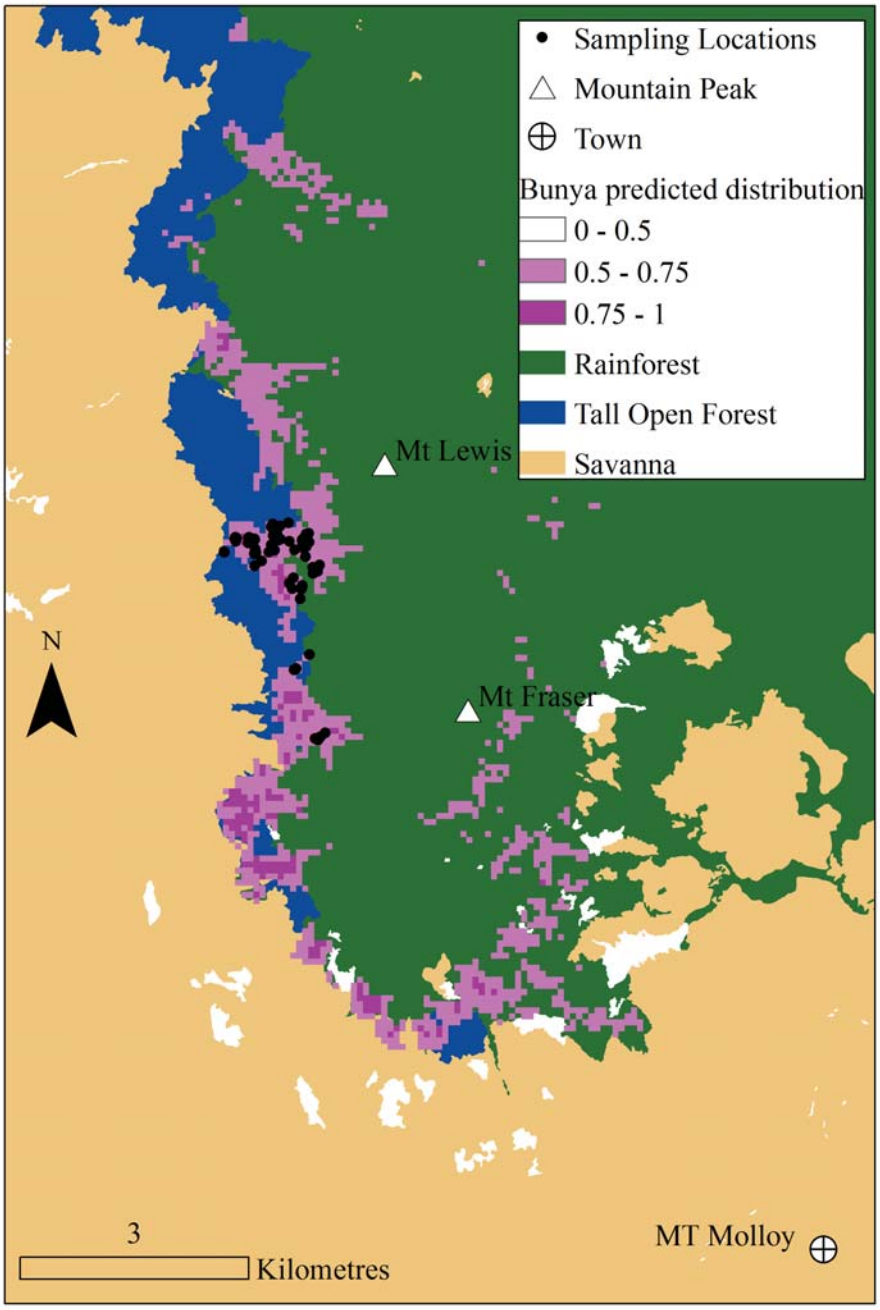
(see following page)


Known Bunya locations
Rainforest
Tall Open Forest
Savanna
Bunya predicted distribution
0 - 0.1
0.1 - 1
Mt Lewis
Cannabullen Falls
N
100
Kilometres

2.3.2 Mount Lewis

Several areas with habitat suitability values between 0.75 and 1 are located along the western and southern escarpments of the Carbine Tableland near Mount Lewis. The SDM predictions of suitable habitat are aligned with the occurrence records for habitat suitability values of 0.5 and above. Potential distribution and habitat suitability values are presented in Figure 10 below.

Figure 10. HSV values (predicted distribution), *A. bidwillii* occurrence records and BVGs for the Mount Lewis – Carbine Tableland area.



SDM predictions for the Mount Lewis area are typically associated with the margins of the rainforest, steep slopes and sub-catchment headwaters although the latter two did not have a significant influence on model performance (Table 2).

2.4 Discussion

The model’s high performance and alignment with the occurrence data reveals a strong association with the rainforest’s western margin. While this is the case for many of the areas with a high HSV throughout the Wet Tropics (Figure 9), it is most revealing and important near Mount Lewis (Figure 10).

Illustrated in the response curves (Appendix 1) for the three most important environmental variables is the effect that these variables have on the model’s ability to predict suitable habitat as the variable changes. The optimal annual mean temperature range is from 15° to 20° while optimal annual rainfall is between approximately 900mm to 1500mm. Distance to rainforest boundary suggests that in either direction, the probability of occurrence dramatically decreases as distance increases, consistent with the behaviour of ecotonal species.

2.4.1 Mount Lewis

High HSVs match known locations of *A. bidwillii* in Leichhardt and Station Creeks. In addition, similar habitats with high HSV were identified in adjacent sub-catchments to the north and south along the western escarpment of the Carbine Tableland.

Proximity to existing stands combined with high HSVs suggests that *A. bidwillii* could remain undetected as small stands or individual trees in adjacent sub-catchments. However, it seems unlikely that these would be as substantive as the known sites in Leichhardt and Station Creeks.

Inspection of high-resolution aerial photography (Queensland Government, 2015) of the study area and adjacent catchments revealed scattered trees with some resemblance to the circular crown structure of *A. bidwillii* with an often-visible centrally radiating branch structure. These characteristics help to distinguish *A. bidwillii* from the surrounding rainforest species. The locations identified in aerial photography are within sub-catchments of Leichhardt Creek and Windmill Creek to the north. However, *A. bidwillii* has not yet been observed in Windmill Creek (P. Stanton pers. comm.) in field surveys.

Aerial photography cannot be solely relied upon however, as *A. bidwillii* is difficult to distinguish amongst tall open forest dominated by *E. grandis.* Future surveys for as-yet un-mapped occurrences of *A. bidwillii* should target tall open forest adjacent to likely rainforest particularly where the two communities meet on steeper slopes.

Generally, the model identified areas with steep to moderate slopes often centred on tributary meetings of small creeks in the headwaters of Leichhardt and other creeks. In most cases this was also the meeting point for tall open forest and rainforest or where rainforest gully vegetation was otherwise surrounded by tall open forest (Figure 10.)

Queensland's regional ecosystem classification system identifies six discreet units or locations of simple notophyll vine forest with emergent *A. bidwillii* (RE 7.12.16) associated with Mount Lewis. While these RE polygons originally formed the basis of fieldwork planning for this project, they do not adequately reflect the size and extent of RE 7.12.16 and they do not capture the distribution of *A. bidwillii* in the area.

There may be small stands or scattered individual trees yet to be documented in sub-catchments adjacent to known stands based on the proximity and near continuity of the high HSV areas illustrated in Figure 10. The absence of *A. bidwillii* from these areas is potentially explained by its poor dispersal ability (Smith & Butler, 2009).

2.4.2 Wet Tropics

There is a very low frequency of suitable habitat for *A. bidwillii* predicted across the Wet Tropics bioregion. The model output for the region identified locations mostly along the western fall of the Great Dividing Range and often in proximity to, or overlapping with, tall open forest particularly along the Carbine Tableland and the Kirrima and Paluma Ranges. In addition, Bakers Blue and the southern area of the Windsor Tableland were identified as potentially suitable habitat. More minor areas of suitable habitat included the western fall of the Lamb Range and the northern area of the Hann Tableland.

While some of these areas are known to support other Araucariaceae including *A. cunninghamii* and *Agathis robusta*, it is highly unlikely that additional geographically disjunct populations of *A. bidwillii* are awaiting discovery.

The model failed to predict the location of the Cannabullen Falls population of *A. bidwillii* in Wooroonooran National Park (Figure 11) as suitable habitat. This suggests that environmental attributes playing a role in the persistence of *A. bidwillii* at this site are different to those occurring at Mount Lewis. Alternatively, a combination of variables not tested within the current model may be more important.

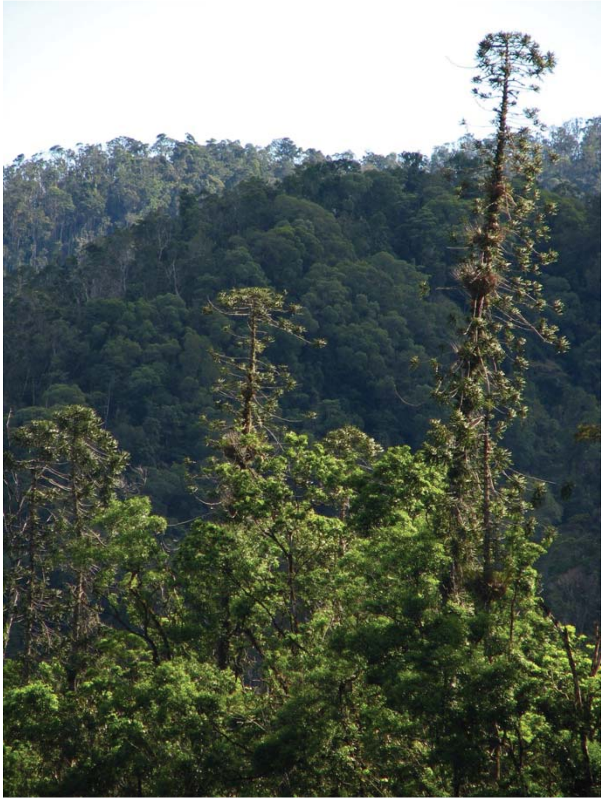


Figure 11. Subpopulation of *A. bidwillii* at Cannabullen Falls, Wooroonooran National Park, Wet Tropics World Heritage Area.

3. Recruitment and Population Structure

Understanding the natural recruitment of the Mount Lewis subpopulation of *A. bidwillii* and its habitat preferences will assist in conservation management and planning. This chapter uses frequencies of size-class data (as a proxy for age) to investigate patterns against two broad models of recruitment: one based on the concept of continuous recruitment and the other that is based on recruitment events occurring in response to disturbance. The results identify recruitment but there is no clear single strategy displayed. While there is an abundance of seedlings, there are very few subsequent size-classes and an almost constant low number of trees between 15cm DBH to approximately 100cm DBH. Interpretation of these results leads to some support for a temporal recruitment strategy interwoven with the vegetation dynamics of tall open forest and rainforest.

3.1 Introduction

Dispersal, recruitment and persistence are the most fundamental challenges faced by all plants (Weiher et al., 1999). Studying natural recruitment is an important step in understanding the ecology of a species or ecosystem as it is essential for species persistence (Newton, 2007). Understanding recruitment patterns is also essential for species or ecosystems that are of conservation significance (Cropper, 1993; Kettle et al., 2012). This is because the type of recruitment pattern a taxon displays, reflected in its population structure, can be used to interpret potential response to disturbance events and inform forest management practices (Newton, 2007; Souza, 2007).

Recruitment can be considered by examining the continuity of the population size or age-class distribution across all individuals. For example, if a population has continuous recruitment, this is often expressed through a reverse J-curve population structure (Hett & Loucks, 1976; Newton, 2007; Veblen et al., 1980). Such a population structure assumes that the number of new recruits is constant and that mortality is equally proportional between size-classes (Newton, 2007). Alternatively, if there are pulses or multi-modal patterns across the population structure, this may indicate recruitment of cohorts triggered by disturbance events (Ahmed & Ogden, 1987).

The study of size-class data as a proxy for age began in the 1970s and continues to be used, particularly in forestry (Newton, 2007) and forest ecology (Aiba et al., 2007; Clark & Clark, 1995; Gibson & Brown, 1991; Johnston & Gillman, 1995; Kelly et al., 2001; Kohira & Ninomiya, 2003; Oliveira-Filho et al., 1996; Peres & Baider, 1997; Singer & Burgman, 1999). As discussed in section 1.3.3, size-class data has been used in ecological studies of population demography in many conifers, particularly members of the Araucariaceae (Enright, 1995; Enright et al., 1999; Kettle et al., 2012; Ogden & Stewart, 1995; Rigg et al., 1998; Souza, 2007).

There are two broad classes of models that have attempted to take demographic information and infer processes relating to recruitment and mortality. These are models that assume either continuous recruitment or models that infer episodic recruitment.

Continuous recruitment of a population has often been implied by evidence of a reverse J-curve population structure (Figure 12) (Hett & Loucks, 1976; Hörnberg et al., 1995; Veblen & Stewart, 1982). Typically, recruitment in these species is not thought to require a disturbance event to trigger the establishment of a new cohort. The reverse J-curve is sometimes referred to as an inverse J-curve (Hett & Loucks, 1976) or a negative exponential distribution (Leak, 1965; Peres & Baider, 1997). A key characteristic of the reverse J-curve population structure is the constant rate of mortality in successive size or age-classes, which can be described by a negative exponential curve (Veblen, 1992). This is also known as a type three survivorship curve, which is the most common in nature (Begon et al., 2006; Newton, 2007; Veblen, 1992).

Negative exponential models have been fitted to size-class data for various tree populations including northern hemisphere conifers (Hett & Loucks, 1976; McCarthy & Weetman, 2006), Chilean *Nothofagus* forest (Veblen et al., 1980) and montane forests in western Kenya (Hitimana et al., 2004). The negative exponential curve fits a y-intercept, the maximum number of individuals in the smallest size-class, while x is asymptotic.

Alternatively, other authors have fitted an inverse power function to the same type of datasets. The power function model assumes a decreasing rate of mortality (Hett & Loucks, 1976; Veblen, 1992) and differs from the reverse J-curve structure because it assumes high mortality rates in the smallest size-classes, followed by decreasing rates of mortality in the larger size-classes (Hett & Loucks, 1976; Singer & Burgman, 1999).

Both the negative exponential and the power function have been employed to support inferences about continuous recruitment. Because both models assume constant recruitment and mortality, evidence for continuous recruitment is most often associated with population structures that are not subject to large, landscape level disturbance events. Thus, a negative exponential or power function representation of age or size-class intervals has long been interpreted as reflecting a stable population within a stable environment (Condit et al., 1998; Leak, 1965; Souza, 2007).

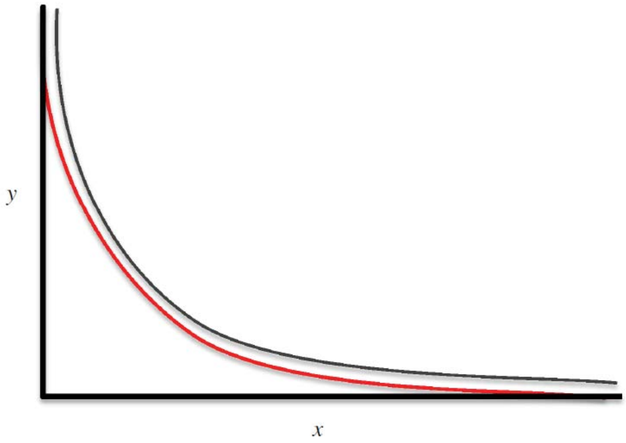


Figure 12. Negative exponential and power function population structures

A reverse J-curve population structure can be expressed by both the negative exponential (red curve) and the power function (grey curve) which are characterised by an abundance (*y*) of lower-end values (*x*) that decline sharply then reach a point where there is very few and are asymptote in shape.

However, some population age and size-class distributions are not well described by negative exponential or power function models. Rather, individuals in age or size-class distributions may exhibit population structures that suggest episodic pulses in recruitment cohorts represented by an overabundance in the smallest categories and a pulse in older age or size-classes not predicted by either of the negative exponential or power function models. Thus, more appropriate models than those used to infer a reverse J-curve population structure are required.

The majority of southern hemisphere conifers, such as *A. bidwillii,* have restricted distributions and predominantly occur in or on the margins of angiosperm-dominated forests. Unlike northern hemisphere conifers, the population structure of southern conifers rarely conform to a reverse J-curve population structure (Enright & Hill, 1995). Early observations in southern hemisphere forests dominated by angiosperms identified gaps in the population structure of conifers (Womersly 1958). Evidence such as this led to the belief that southern hemisphere conifers were suffering from widespread regeneration failure (Ogden, 1985). For example, based on evidence from recruitment patterns Womersly (1958) suggested the *Araucaria* spp. in the mixed forests of the Australia-Pacific region were relicts in decline, and that this decline was a function of superior competitive abilities of angiosperms.

However, missing from early observations of southern hemisphere conifers, often observed in rainforests, was an understanding of succession and forest dynamics (Enright & Ogden, 1995; Ogden, 1985). The persistence of a number of coniferous taxa from southern temperate latitudes through to the humid equatorial tropics appear to be driven by a common factor; major disturbance (see, for example: (Burns, 1993; Cullen, 1987; Ogden & Stewart, 1995; Souza, 2007). Ogden (1985) developed a theoretical framework to account for the presence and persistence of light-demanding canopy or emergent species in warm temperate rainforest that did not predict population structures consistent with the reverse J-curve pattern. This theoretical framework, known as the “temporal stand replacement model” (Ogden, 1985), has become an important theory in identifying the recruitment strategies of Araucariaceae and other southern conifers growing in rainforest habitats (Enright et al., 1999). Primarily, this model is centred on the occurrence of a disturbance event substantial enough to allow patch size recruitment of a cohort of light-demanding species.

In Ogden’s (1985) initial study, extensive areas of *ca.* 100 year-old regrowth *Agathis australis* were considered to be the species’ natural response to catastrophic, landscape level disturbance. Based on the temporal stand replacement model, cohorts of *Agathis australis* established after a major disturbance event may give rise to three or four successive generations. Eventually, by about the fifth generation of recruitment post disturbance, dominance of *Agathis australis* is eroded through competition with angiosperms. Ogden (1985) proposed that this process takes greater than 1000 years and included within the theory is the potential for a major disturbance event to occur at any stage following the peak of basal area of the first generation (Figure 13).

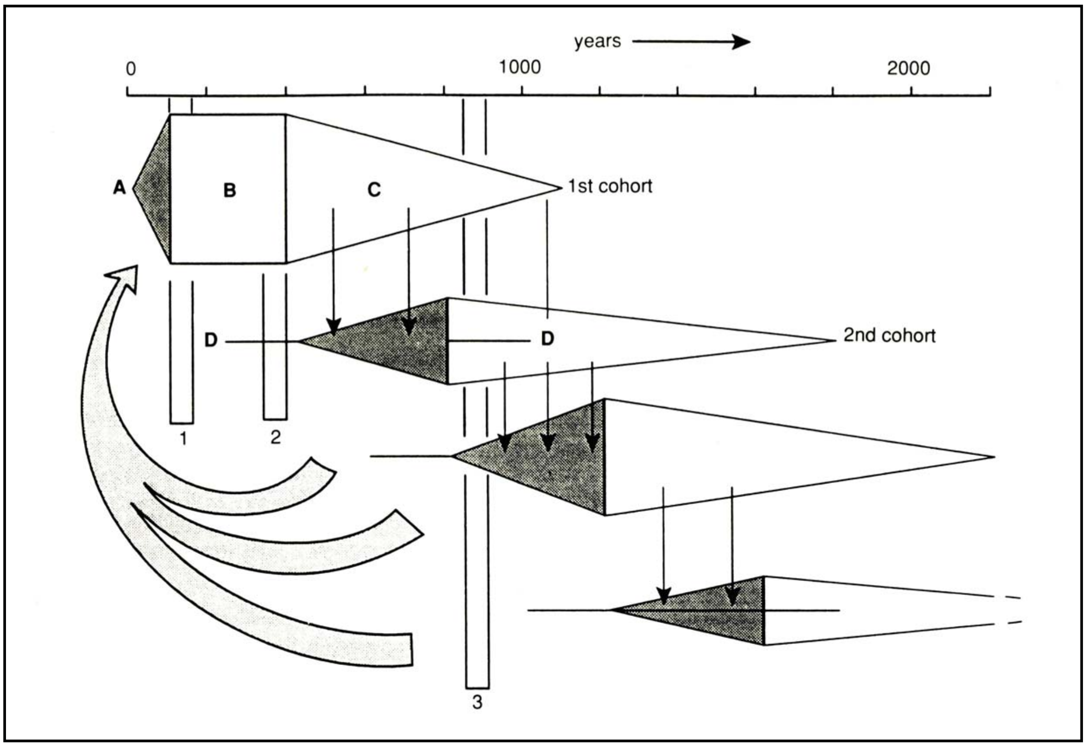


Figure 13. **The Temporal Stand Replacement Model**

The temporal stand replacement model (Ogden & Stewart 1995) was developed to explain possible processes operating on *Agathis australis* forest that drive recruitment. Each unit of cohorts is represented by the four lozenge-shaped-blocks illustrated above. At the beginning of the process a major disturbance event occurs which initiates mass recruitment. This is represented by **A** (the shaded area) in the first cohort. The expansion of **A** represents a mass recruitment cohort increasing in biomass to a point where thinning and a decline in numbers is matched by increasing biomass of survivors, represented by **B**. Whilst still only concerned with the first cohort we begin to see a decline in abundance and biomass as the original population becomes senescent at **C**. However, the senescent phase, where the canopies typically become more open and trees begin to collapse can give rise to a second generation cohort at reduced densities. **D** illustrates the second generation. The phase of the population in time represented by **D** potentially supports the maximum amount of biomass and the most complex age structures. It is possible a third generation could arise whilst the first generation persists. This is expressed through vertical arrows, which illustrate gap formation processes. The thick three-tailed arrow expresses a stochastic disturbance event exogenous to the collapse and recruit processes operating within. Vertical columns 1, 2 and 3 indicate 50-year intervals.

Inherent in the above model is the prediction that recruitment pulses should be apparent in the size or age-class population structures. There is evidence that the model is a good fit in explaining the regeneration strategies for a number of *Araucaria* from New Guinea, New Caledonia and South America that includes *A. hunsteinii* and *A. laubenfelsii* (Enright et al., 1999) *A. araucana* (Veblen, 1982) and to a lesser extent *A. angustifolia* (Souza, 2007).

Nevertheless, there are no comparable studies undertaken on Australian Araucariaceae. The little research that has been done on *A. cunninghamii* recruitment strategies suggests that there is some expression of continuous recruitment across different habitats (Enright & Ogden, 1995). While some work has been done on the regenerative capacity of *A. bidwillii* in regrowth forests of South East Queensland (Smith & Butler, 2009), the research described in this chapter aims to investigate the population size-class distribution of *A. bidwillii* across two habitats in Far North Queensland and examine the data for evidence of continuous or episodic recruitment behaviour.

3.2 Methods

3.2.1 Field Sampling

Data was collected from 13 sites comprising tall open forest and rainforest throughout the Leichhardt Creek catchment over a three-year period (Figure 14). Stratified random sampling ensured variation in aspect and vegetation, while site selection was dependent on the occurrence of *A. bidwillii*. Based on prior knowledge of the catchment and knowledge of the extent of *A. bidwillii* to be predominantly in rainforest, more study sites were intentionally located in the rainforest BVG than in the tall open forest BVG (described in section 1.3.2) (Table 3), consistent with the approach of stratified random sampling (Newton 2007).

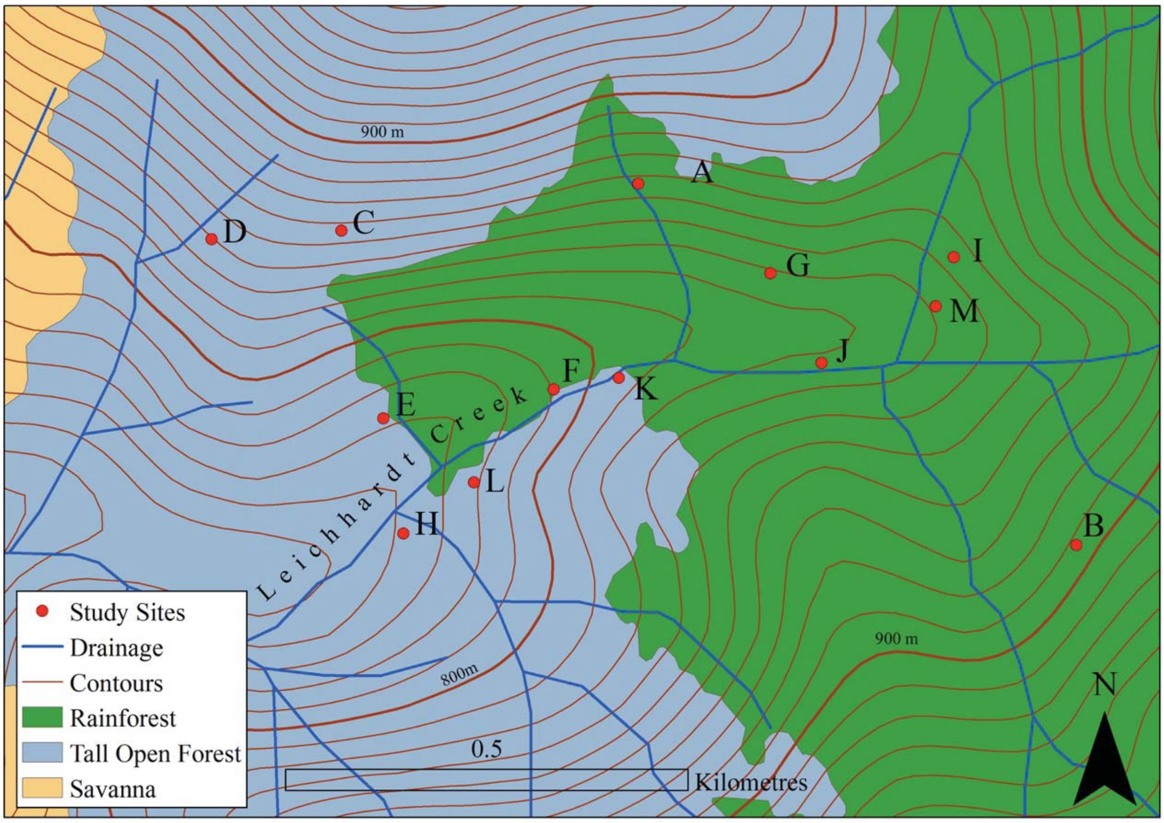


Figure 14. **Leichhardt Creek field sampling sites A-M (13).**

Sampling site design

1. 20x20m	2.	3.	4.
5.	6.	7.	8.
9.	10.	11.	12.
13.	14.	15.	16.

80x80m

Figure 15. **Sampling site design and plot arrangment.**

Upon location of areas containing *A. bidwillii*, square sites of 0.64 hectares were established. In all cases attempts were made to ensure individual sites were established across homogenous terrain and habitat type (Figure 15). Variation to this approach occurred primarily in areas where homogeneity of environmental characteristics such as rocky outcrops resulted in the 0.64 hectare square sampling site being impossible to establish. In these circumstances sampling sites were reduced in size to avoid the local variation in terrain. Summary data including size, location, vegetation and common species for each site is contained in Appendix 2.

All sites were divided into 20 x 20 m plots and marked with flagging tape. Each plot was then systematically searched for *A. bidwillii* by traversing in a roughly circular clockwise direction from near the plot boundary to the plot centre. All individuals encountered were measured for diameter at breast height (DBH). Stem diameters for individuals less that 2m in height were measured at 20cm above ground or recorded as a seedling. Consistency of search rigour was maintained by an allocation of 15 minutes for each plot excluding note taking and time taken to measure DBH. Time was increased above 15 minutes when dense vegetation of *Calamus* spp. and *Dendrocnide moroides* (stinging tree) were encountered. In these instances, more time was located to visual searches. Rockiness was also visually measured and sites with >50% rock cover were considered rocky.

Table 3. Study site and sampling summary

		Number of sites	Total Area (ha)
BVG	Rainforest	8	4.4
	Tall Open Forest	5	2.88

Seedlings, defined as anything <2cm in stem diameter and <2m in height were excluded from the population structure analyses. This was done to avoid over-inflated smaller size-classes due to a seedling bank of individuals that could range in age from less than a year to perhaps 10 or more years old.

Size-class data is presented for all sites to provide an illustration for the Mount Lewis population overall, then in each BVG of tall open forest and rainforest, then for rainforest sites that are split into either rocky or non-rocky.

3.2.2 Limitations

Size-class was chosen as a proxy for age because of the ease within which it can be obtained from a large sample population. However, this approach has several limitations and there is the unavoidable potential that trees of the same age are spread over several size-classes reducing the reliability population structure interpretation. While accurate measures of age provide the opportunity for more robust analysis, they are not as easily obtainable as size.

Natural variation in growth rates can result in widely different size measurements for trees of the same age (Newton, 2007; Ogden, 1985). Often, age estimates reliant on size-class data are accompanied by dendrochronological quantification that may include tree ring counts or radio carbon dating obtained from core sampling. In long-term studies, measuring growth-rates may also yield data on tree age (Newton, 2007).

While there will be some variation and undoubtedly error in age inferences, precise age estimates weren't considered necessary for this study. In addition, core sampling multiple large, presumably old trees of a very restricted population was not justified for this project.

3.2.3 Statistical Approach

As previously mentioned, earlier studies have used linear regression of the number of individuals in size-class frequencies to test both negative exponential and power function models. Fitting these functions requires log-transformation of frequency (negative exponential) and log transformation of both frequency and size-class (power function), which is used to linearize the relationship. While some authors advise against log transformation of a response variable such as count data in favour of generalised linear models, log transformation followed by least-squares linear regression has recently been shown to be robust over a wide range of conditions (Ives, 2015).

I began by testing the fit of the two models that assume constant recruitment and mortality; i.e. the negative exponential and power function models. Each model was generated using the full set of explanatory variables obtained from fieldwork (size-class, BVG and rockiness) and all possible interactions.

After fitting the full model, I used backward step-wise regression to remove all non significant terms until the minimum adequate model – the model with fewest significant terms – was reached using the Drop1 command (R Development Core Team, 2012).

To examine whether the negative exponential or the power function was the more likely explanation of the data, I then compared the models determined above based on information theoretic criteria (Akaike's Information Criteria or AIC) (Burnham & Anderson, 2002), accepting as the best representation the model that returned the lowest AIC.

Whether or not a linear model identifies particular terms as significant and whether one model is preferred over another, is not an indication that the model is a good description of the data, however. In order to examine the appropriateness of the models for the data, I therefore examined the residuals from the model identified as the more likely explanation of the data and tested for significant curvature in residuals from the model by fitting a smoothing curve to residuals across size-classes. Significant curvature indicates pattern in residual distribution after the removal of the expectation of either the negative exponential or power models. In this way it can identify deviations from either model. Smoothing curves were fitted in Mixed GAM Computation Vehicle (MGCV) (Wood, 2014).

Although excluded from the above analysis, seedlings provide a valuable additional dataset that can yield further insights into the ecology of *A. bidwillii*. After log-transformations failed to improve normality, I tested for differences in the density of *A. bidwillii* seedlings between tall open forest and rainforest BVGs using a Kruskal-Wallis one-way ANOVA on ranks. I estimated density by averaging the total number of records in seedling size-classes and scaling this by the sample area to produce a per-hectare figure consistent with forestry standards (Newton 2007).

In all treatments I aggregated the data from each of the 13 sites into BVGs. The rationale behind this is based on the objective of identifying population structures across habitats. While undertaking fieldwork for this project it became clear that *A. bidwillii* did not occur in discrete and separate stands as speculated, but is found across suitable habitat in a more or less continuous way as illustrated in Figure 8. Therefore, I considered that the best way to identify patterns and population structures in either rainforest or tall open forest was with aggregated data.

3.3 Results

Overall, the Mount Lewis subpopulation of *A. bidwillii* displays a pattern in population structure that is indicative of the negative exponential model. It is characterised by an abundance of plants in the smallest size-classes and very few to single individuals in the larger size-classes (Figure 16).

3.3.1 Population Structure

As an initial approach, frequency histograms of individuals within size-classes were produced to display population structures. These are presented in a series of graphs beginning with all sites combined, then individually for tall open forest and rainforest. Rainforest is broken down further into rocky and non-rocky population structures. The aggregated frequency data for all 13 study sites is presented in Figure 16 below. Frequency histograms for each site are presented in Appendix 3.

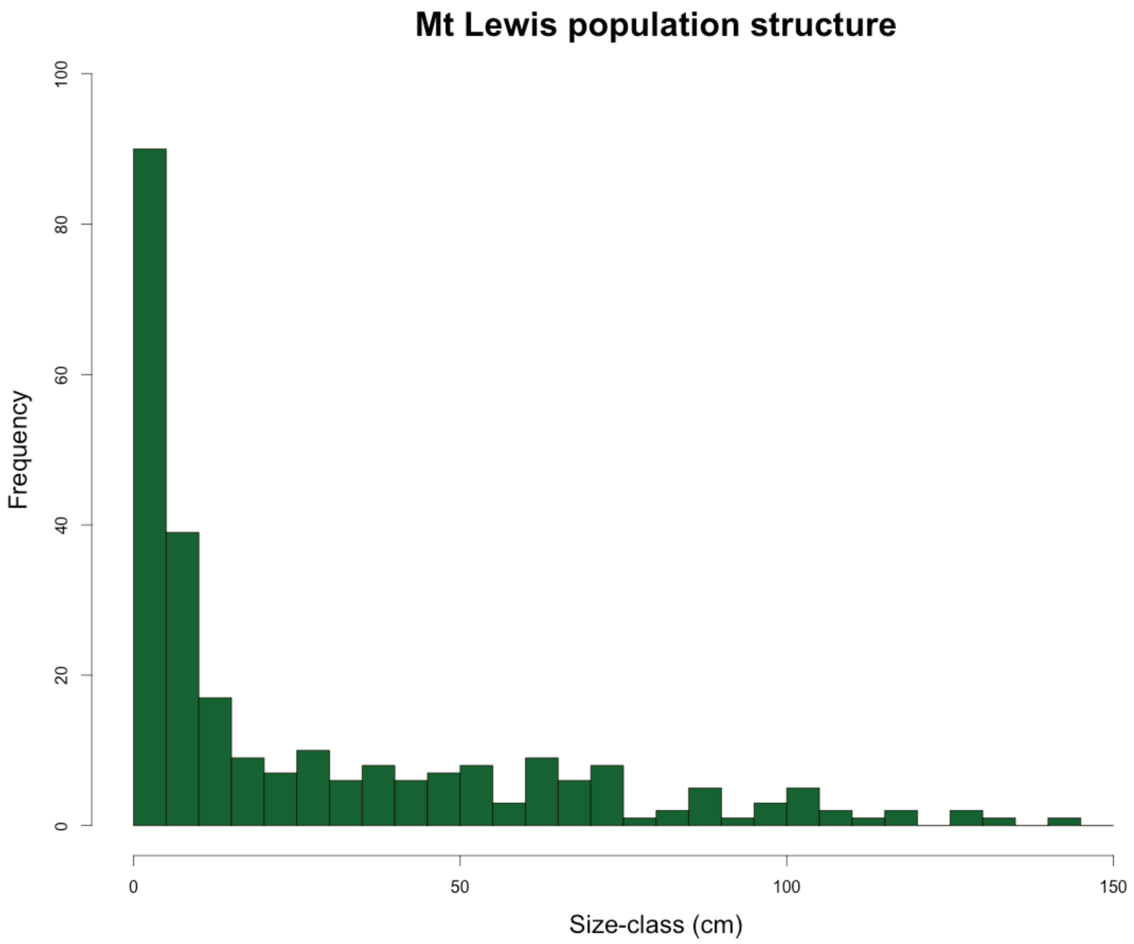


Figure 16. **Size-class (DBH) frequency data for *A. bidwillii* at 5cm intervals excluding all seedlings <2cm in stem diameter.**

Presented in 5cm intervals, the size-class frequencies are useful in identifying key points along the population structure spectrum. After the 15cm size-class, frequencies are somewhat consistent until approximately 80cm DBH, then much reduced except for a pulse around 100cm DBH before tapering off.

When rainforest and tall open forest are considered individually, there are differences between patterns displayed in each BVG (Figure 17). For example, within the tall open forest BVG, *A. bidwillii* is abundant in the smaller size-classes before a sudden decrease in abundance in successive size-classes. While there is a small increase associated with mature trees from approximately 30cm DBH, there were no trees recorded above 85cm DBH in tall open forest. The lower panel in Figure 17 (below) presents the frequency data for *A. bidwillii* across the rainforest BVG. Within this BVG, *A. bidwillii* is less abundant than it is in tall open forest across all size-classes until 75cm DBH. After this point, *A. bidwillii* becomes relatively more abundant with increasing size up until the 145cm size-class. The largest tree measured was 144cm DBH. The key difference in the aggregated data for the rainforest sites is far fewer smaller size-classes and a longer tail of larger size-classes.

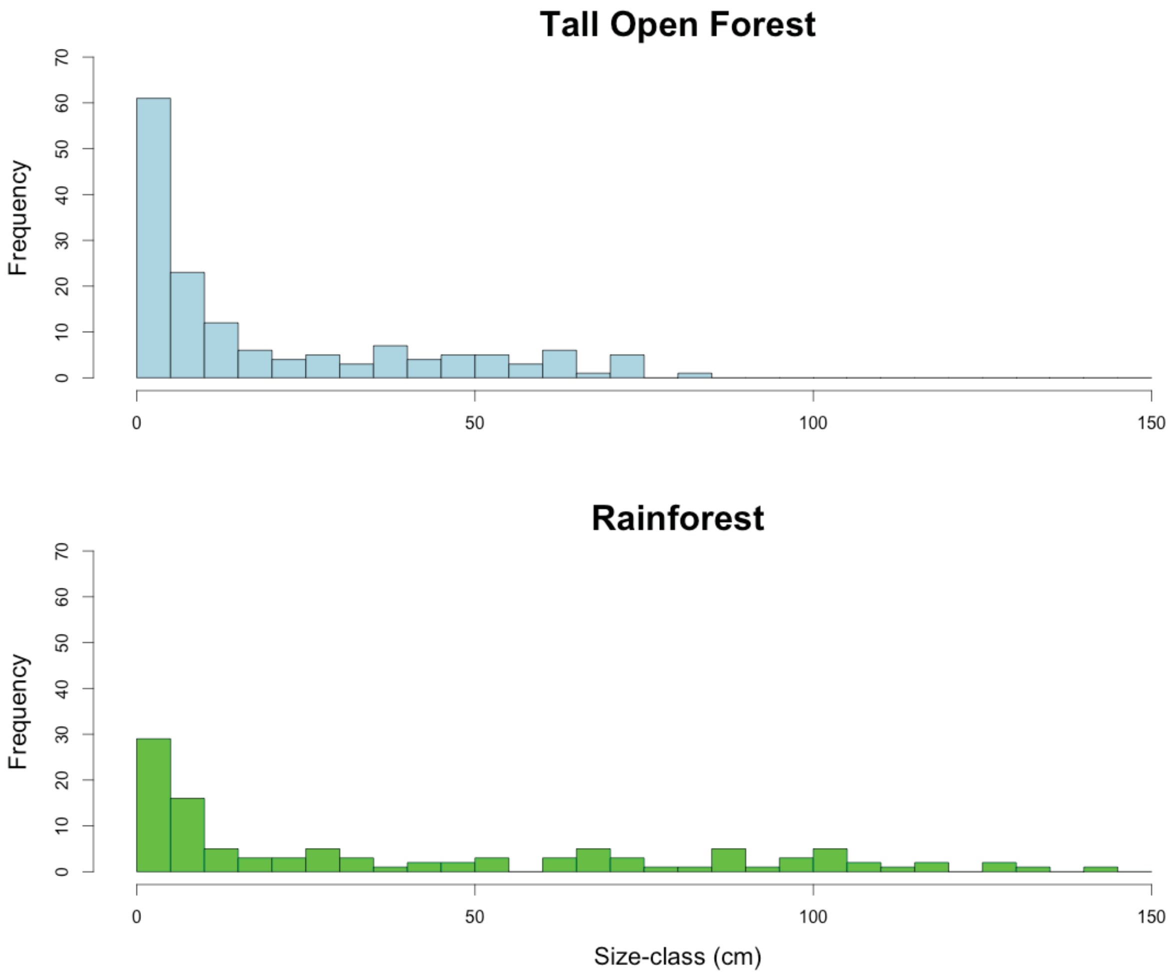


Figure 17. **Size-class (DBH) frequency distributions for *A. bidwillii* in tall open forest and rainforest at 5cm intervals excluding seedlings.**

In both of these size-class data subsets, it appears that the rate of mortality between size-classes is greater than what may be supported in a continuous recruitment scenario. Most mortality is occurring within the first 20cm (DBH) size-classes after which there is a general levelling off in abundance.

Two of the rainforest sites had a high amount of surface rock cover and were observed to support an increased abundance of *A. bidwillii.* I created a further subset of the data to inspect any potential differences in population structure between rocky and non-rocky (well-developed) rainforest. When rocky and non-rocky rainforest sites are considered individually, there are differences between patterns displayed in each subset of data (Figure 18). For example, within the rocky rainforest data, *A. bidwillii* is abundant in the smaller size-classes before a sudden decrease in abundance in successive size-classes. While numbers are still low, there is a sharp increase around 70cm DBH followed by minor occurrences at 80 cm and 100cm DBH. The second graph in Figure 18 below presents the frequency data for *A. bidwillii* in well-developed rainforest. Within this subset of data, *A. bidwillii* is again less abundant across all size-classes. However, gaps in the population structure emerge after 10cm DBH and there is a marked increase at around 100cm DBH. The key difference in the data for well-developed rainforest sites is a very low number of the smallest size-classes, evidence of a gap in recruitment and the suggestion of a recruitment pulse at around 100cm DBH. This is typical of a modal or pulse recruitment pattern and shares features with the temporal stand replacement model. Seedlings are generally sparse with less than 20 individual plants observed.

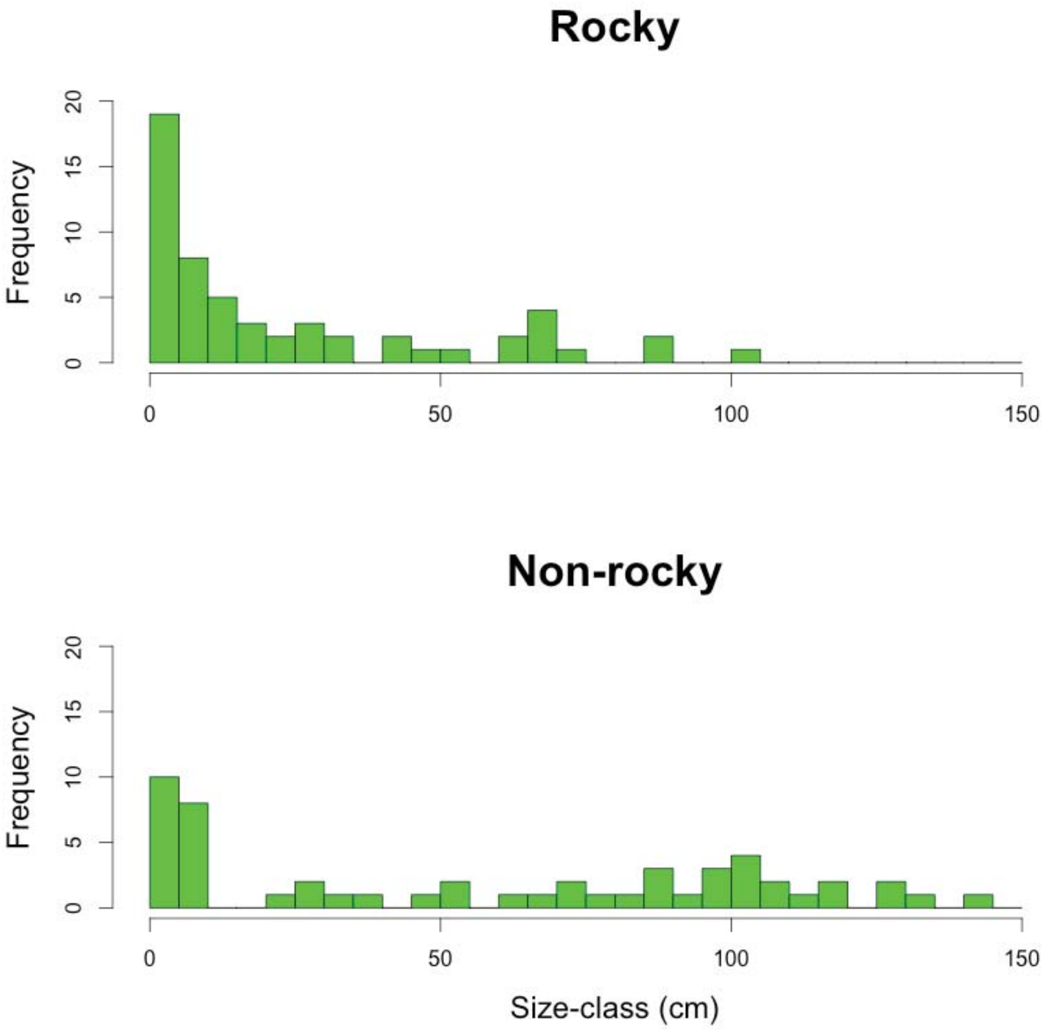


Figure 18. **Size-class (DBH) frequency distributions for *A. bidwillii* in rocky and non-rocky rainforest at 5cm intervals including seedlings.**

3.3.2 Linear Regression Analysis

For both the power function and the negative exponential models, the minimum adequate model included the two variables (terms) “size-class” and “BVG” and their interaction. The negative exponential model was considered best of the two alternatives based on AIC (AIC $_{\text{negative exponential}}$ = 92.11, AIC $_{\text{power function}}$ = 147.70). The interaction between size-class and BVG was significant ($F_{1,134} = 5.96$, $P = 0.05$) as was the main effect of size-class ($F_{1,134} = 38.89$, $P < 0.001$), however the main effect of BVG on its own was not ($F_{1,134} = 0.002$, $P = 0.1$). BVG must be retained as the main effect, however, because of the significance of the interaction term. Table 4 shows the coefficients for each term.

Table 4. **Negative exponential model.**

Variable	Coefficients (SE)	T value	*P*
Tall Open Forest	1.11(0.14)	7.821	0.000
Size-class	-0.02 (0.004)	-4.858	0.000
Rainforest	-0.36 (0.2)	-1.865	0.1
Size-class: rainforest	0.01 (0.004)	2.385	0.05

The differences in population structure based on the fit of the negative exponential model between rainforest and tall open forest were evident (Figure 19). For example, the rainforest data displays a longer, gentler slope with a logged frequency intercept of 0.74. In contrast tall open forest has a logged frequency intercept of 1.12 and is displays a sharper and shorter decline as expected from the significant interaction.

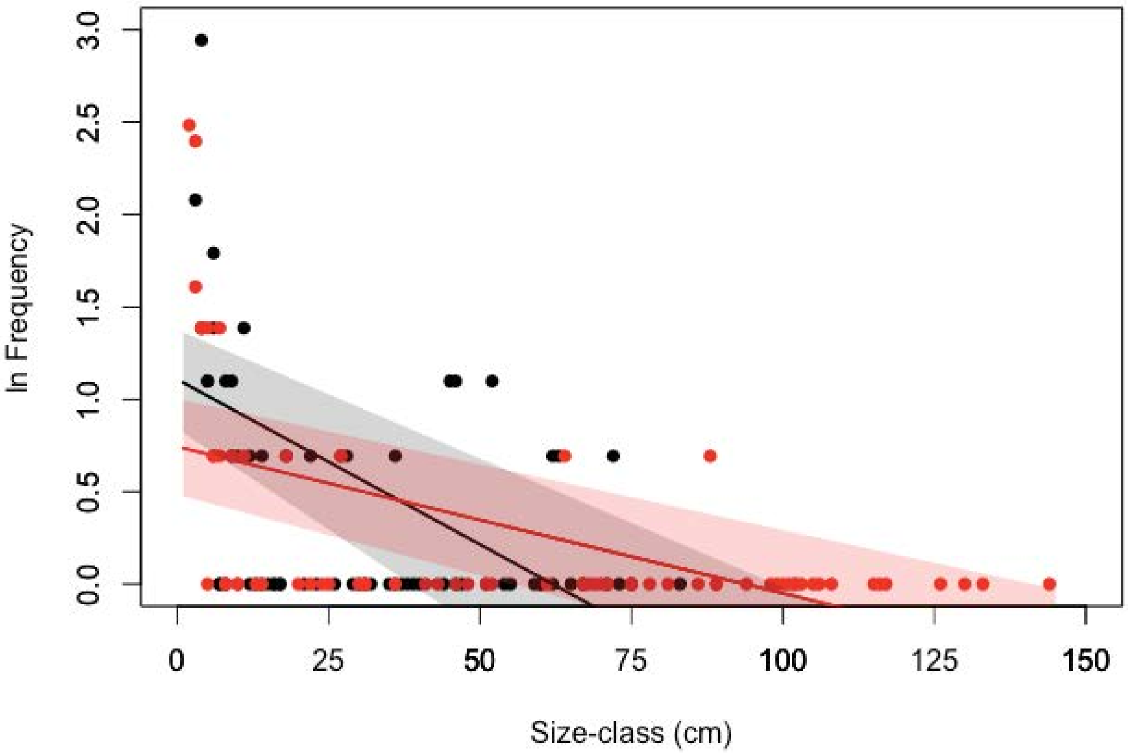


Figure 19. **Fit of the negative exponential model to size-class data in rainforest and tall open forest sites.**

Rainforest (red) has a significantly lower intercept and longer tail than tall open forest (black).

Examination of the residuals, however, reveals that the negative exponential does not fully explain the distribution of the size-class data and is a relatively poor fit (Figure 20). The smoothing curves fitted to residuals for both rainforest and tall open forest were significant, indicating pattern of locations along the size-class spectrum where there were greater and fewer numbers of individuals than expected from the negative exponential model alone (the estimated degrees of freedom (edf) (indicative of amount of curvature) was 7.452, F =11.47, approximate significance of the smoothing term P <0.001 for tall open forest, and edf = 8.402, F = 8.898, P <0.001 for rainforest). The smoothing function could explain 63.6% of the deviance of residuals for tall open forest and 59.6% of the deviance in rainforest. Because the span along the size-class axis differed between BVGs (see Figure 19 above), no formal test of similarity between smoothing functions could be made. Nevertheless, evident within the fitted smoothing curves are clear low points where residuals show wave-like pulses. Such patterns of wave-like pulses suggest events that allow recruitment cohorts to escape the seedling bank at particular points in time, rather than continuously. This is more consistent with the temporal stand replacement model in which recruitment cohorts are triggered by an event expressed by pulses in age or size-classes within the population structure.

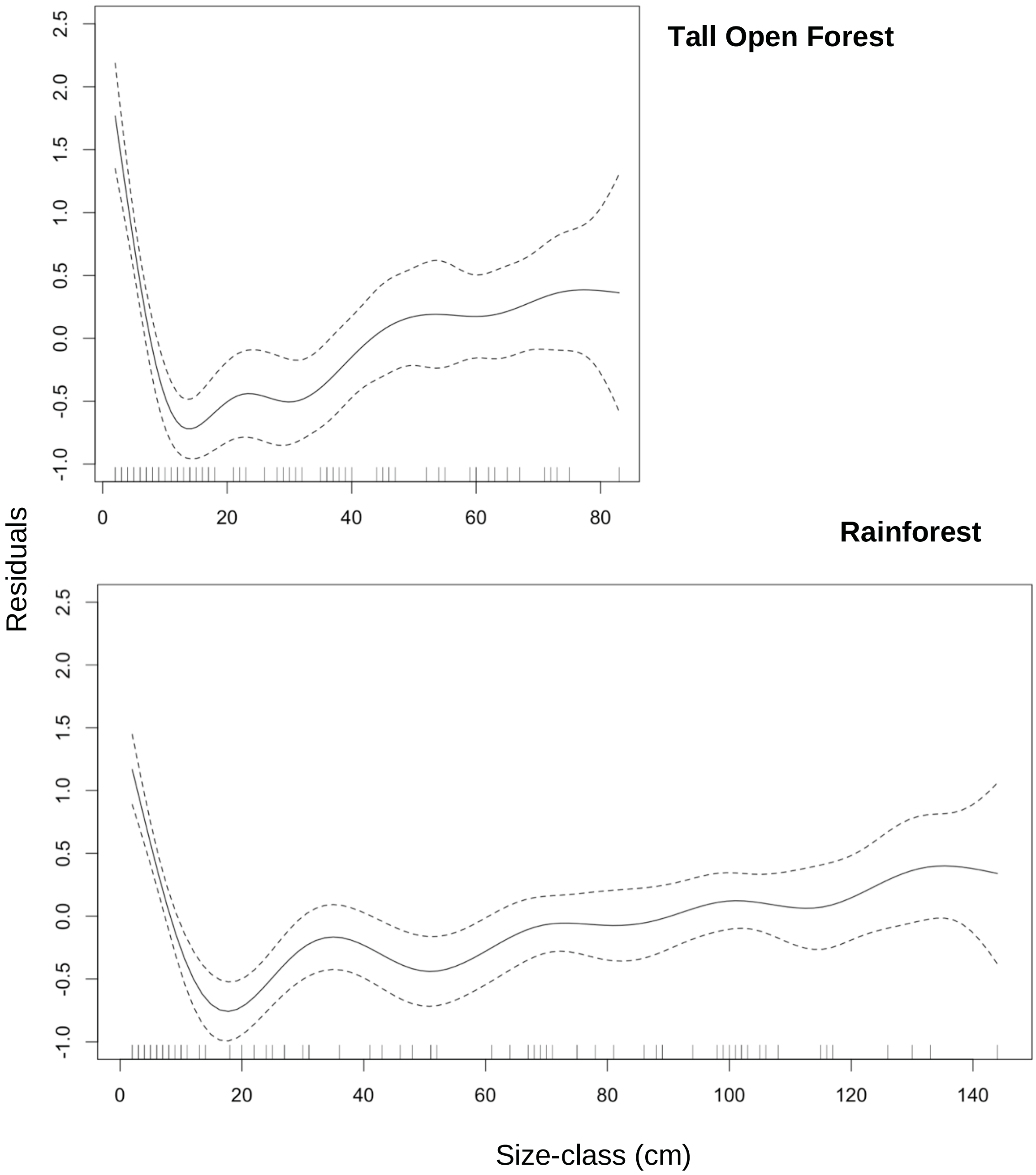


Figure 20. **Fit of the smoothing function of residuals from the negative exponential model describing frequency of individuals against size-class.**

The smoothing function shows significant curvature in residual distribution, indicative of wave-like pulses.

3.3.3 Density

The density of *A. bidwillii* seedlings varied significantly between tall open forest and rainforest. A Kruskal-Wallis one-way ANOVA on ranks identified a significant difference ($H_1 = 6.549$, $P = 0.01$) in the median density values of seedlings between tall open forest and rainforest (Figure 21).Tall open forest had median density of 75 seedlings per hectare (25th quantile = 25, 75th quantile = 100). Rainforest had a median density of 25 seedlings per hectare (25th quantile = 25, 75th quantile = 50).

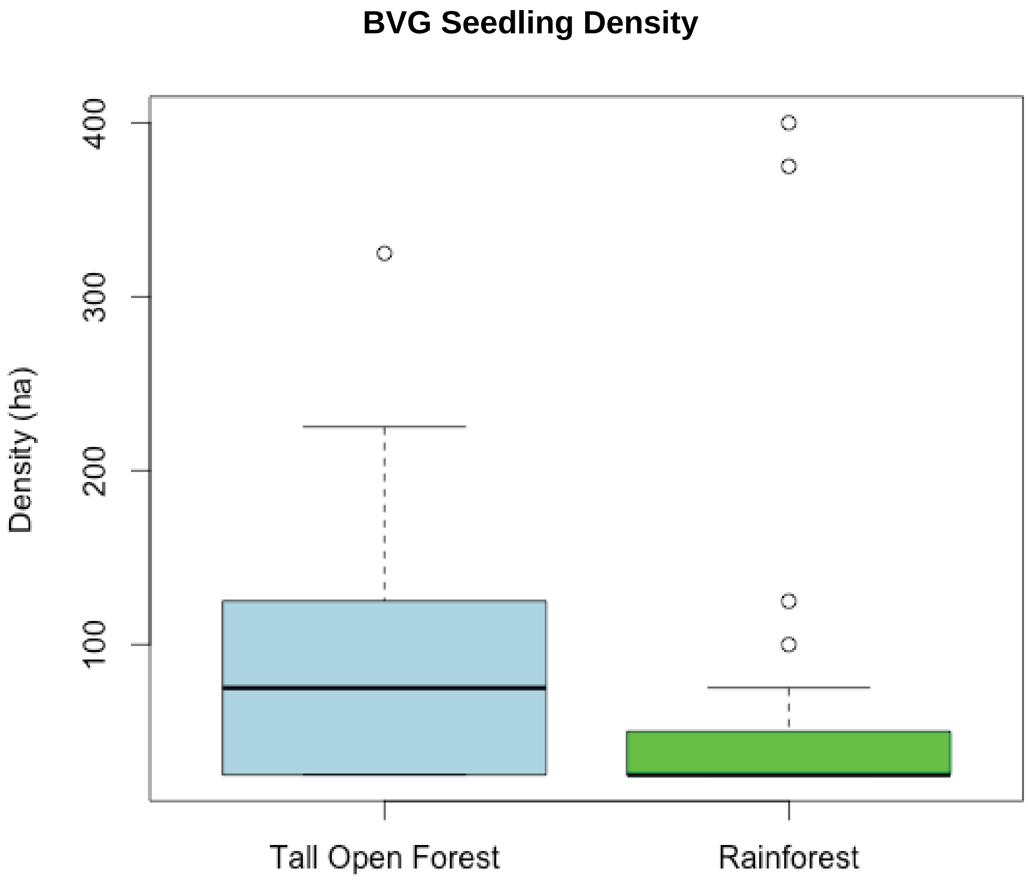


Figure 21. Box plot showing the median seedling density per hectare between BVGs.

3.4 Discussion

The aim of this chapter was to examine the population structure of *A. bidwillii* to identify evidence of recruitment within the Mount Lewis subpopulation and to investigate if recruitment processes were different between habitats. While there is evidence of recruitment there remains some uncertainty about the type of strategy revealed in the population structure. Evidence of recruitment is represented by the occurrence of all critical size-classes within the aggregated frequency data from seedling to reproductive adults (Figure 16). Although resembling a reverse J-curve structure, it is inappropriate to make assumptions about the likelihood of recruitment from this histogram. What is clear from the aggregated data from all 13 sites is that within the sample population a relatively small number escape the seedling bank to go on to larger size-classes.

Inspection and analysis of the data subsets for each BVG revealed observable and significant differences. Again, frequency histograms for each BVG (Figure 17) illustrate reverse J-curve population structures; but these are merely observations and cannot be relied upon to draw any conclusions about the recruitment of *A. bidwillii.* By fitting the negative exponential model, often used to test for continuous recruitment, to each subset I was able to assess the appropriateness of the model and test for significant interaction between vegetation, rockiness and size-class. As suspected, there are differences in both the abundance of *A. bidwillii* in some size-classes and these interaction terms within the model and between the models (for each BVG) (Table 4, Figure 19).

The smoothing curves fitted to the residuals in Figure 20 illustrates that the negative exponential model does not explain the distribution of data. Subsequently, assumptions of continuous recruitment are not supported by evidence. The significance of the curves for both tall open forest and rainforest BVGs and the wave-like pattern in Figure 20 suggests that there are periods where there is some escape from the smaller size-classes alternating with an unknown limiting factor. This could be seed availability associated with masting events or niche availability due to a stochastic event but these remain to be investigated. Cohorts of seedling establishment associated with masting events were not detected and are likely masked within the seedling bank.

Tall open forest represents important habitat for *A. bidwillii*, which is able to establish and persist until maturity within this BVG. The tall open forest population structure is characterised by an abundance of seedlings and a greater number of size-classes around 20cm DBH as illustrated in Figure 17 (above) and Figure 22 (below). The largest tree in tall open forest is 84cm DBH whereas the largest tree in rainforest was 144cm DBH. The long tail of larger size-classes in rainforest, evident in both Figures 19 and 20 (above) are a key difference in the population structures between the two BVGs. Although age estimates based on size-class should be treated with caution, this suggests the establishment of *A. bidwillii* is potentially younger in tall open forest than in well-developed rainforest.

Figure 22. Juvenile (pole) sized *A. bidwillii* recruitment in tall open forest, indicated by the red arrows.

The profile of *A. bidwillii* size-classes across the tall open forest – rainforest gradient is suggestive of a potential recruitment process that may span centuries. For example, well-developed rainforest supporting >50m emergent *A. bidwillii* with >100cm DBH may have been tall open forest when the trees became established several centuries ago. In a study on the relationship between growth rate, tree rings and size-class, Ogden (1981) estimated the age of *A. cunninghamii* on the Atherton Tableland to be 304.6 years at 120cm DBH.

Despite a greater survey effort in rainforest, *A. bidwillii* seedling density is significantly lower than for tall open forest. While the largest trees occur in rainforest and presumably produce greater volumes of seed, the paucity of seedlings observed within many rainforest sites that included these large trees is perplexing. However, predation of other rainforest seeds (i.e. *Elaeocarpus bancroftii*) by rodents was conspicuous in the rainforest leading to the conclusion that such a fate would also befall *A. bidwillii*.

Further, most of the recruitment in rainforest occurs on sites where there is a high cover of surface or near surface rocks impeding the development of rainforest species. These rocky sites can also become structurally dominated by *A. bidwillii*, which suggests the edaphic conditions give it a competitive advantage over angiosperms. This is consistent with one of the conifer recruitment strategies summarised by Brodribb et al. (2012) although at a very localised scale.

Rocky sites where *A. bidwillii* is abundant and structurally dominant may act as a refuge or source population over time and may have their own population dynamics occurring. However, inferences about age from size-class data in these environments should be treated with significant caution arising from the natural variation in growth rate likely to occur due to edaphic conditions.

Removing the rocky sites from the rainforest data reveals another important aspect of the population for *A. bidwillii.* Figure 18 (above) displays the size-classes for the two subsets of rainforest data; rocky and non-rocky. Rocky sites resemble tall open forest in their size-class profiles, which also displays the reverse J-curve population structure.

In contrast, the size-class profile for the remaining rainforest sites departs from any resemblance to the negative exponential. With less than 20 individuals in size-classes <20cm and a clearly evident spike in trees at 105cm DBH, there is evidence of a past recruitment cohort that may have established under different environmental conditions. This shares some consistency with the temporal stand replacement model first described by Ogden (1985), and later by Ogden and Stewart (1995). A key difference however is that *A. bidwillii* is found as scattered individuals as opposed to a patch or stand of trees. As scattered individuals, there is also potential that there is variation in growth of *A. bidwillii* in response to localised disturbances arising from tree-fall, defoliation from cyclones or drought.

Notwithstanding the limitations of estimating age from size as identified by Ogden (1981), there is a likelihood that the current population of the largest *A. bidwillii* may have established between 300 to 500 years ago based on the age estimates of other Araucariaceae.

This is one of the first Australian studies to investigate the population structure and potential recruitment patterns of *A. bidwillii.* The results presented here indicate that while recruitment may be observable, it is far from certain how this occurs over time and space. Further research is obviously required to better understand recruitment patterns and how they relate to or are part of the temporal nature of forest succession and dynamics.

4. Conservation Assessment

Presently, *A. bidwillii* is listed by the IUCN as least concern (lc). This assessment is based on consideration of the entire population as one taxonomic unit, inclusive of both the Wet Tropics and the South East Queensland subpopulations. With consideration given to the contemporary stabilisation of past threats and the inclusion of most stands within the protected area estate, *A. bidwillii* is not considered to be at risk of extinction (Thomas, 2011).

However, as a genetically distinct subpopulation with observed morphological differences (Pye, 2005) and facing its own unique threats (Thomas, 2011), there is a demonstrable need to assess the conservation status of the Mount Lewis subpopulation of *A. bidwillii* (referred to in this chapter as *A. bidwillii* (Mt Lewis)).

This chapter investigates the conservation status of *A. bidwillii* (Mt Lewis) using the methodologies applied to a species, other taxonomic ranks, subpopulations and ESUs using IUCN assessment tools, standards and criteria to answer the following research question:

What is the conservation status of the Mount Lewis subpopulation of A. bidwillii?

4.1 Introduction

Globally, biodiversity is under increasing threat and many leading scientists describe this process as the sixth great extinction event (Ceballos et al., 2015). This threat to biodiversity is increasingly recognised as a priority in Australia’s policy framework (Natural Resource Management Ministerial Council, 2010) and public discourse (Flannery, 2012).

Both international and domestic initiatives to address threats to biodiversity have arisen from the United Nations Convention on Biological Diversity (the Convention) of which Australia is a signatory. The Convention and Australia’s supporting policy and legislative framework defines biodiversity as the natural genetic, taxonomic and ecosystem diversity found within the landscape (Natural Resource Management Ministerial Council, 2010).

In response to increasing threats to biodiversity at a global scale, the IUCN developed the Red List of Threatened Species (the Red List) in 1964. The goal of the Red List is to: "*provide information and analyses on the status, trends and threats to species in order to inform and catalyse action for biodiversity conservation*" (IUCN Red List Committee, 2013).

The Red List is an internationally recognised and critical tool in establishing priorities for the conservation and management of threatened species in all countries and jurisdictions. It rates species and other taxonomic units along the following categorical delineations: not evaluated (NE), data deficient (DD), least concern (LC), near threatened (NT), vulnerable (VU), endangered (EN), critically endangered (CR), extinct in the wild (EW) and extinct (EX). For a taxon to be considered threatened it must meet the criteria for vulnerable, endangered or critically endangered (IUCN Standards and Petitions Subcommittee, 2014).

Ascribing a taxon to any of the above categories requires assessment against a set of criteria set out in *Guidelines for Using the IUCN Red List categories and Criteria* (IUCN Standards ad Petitions Subcommittee, 2014).

The information I have relied upon in this assessment of the Mount Lewis subpopulation is based on quantified data, inferred observation and personal communications. The limitations of this approach are acknowledged and are not considered conclusive.

4.1.1 Justification

Although the IUCN's Red List Categories and Criteria can be applied to any taxonomic unit at or below the species level, taxa below the rank of variety, including form, morph or cultivar are excluded from the Red List. However, subpopulations represent an exception to this rule and warrant assessment when there is no exchange of individuals with other subpopulations (IUCN Standards and Petitions Subcommittee, 2014).

Maintaining the genetic diversity of species is a fundamental tenet of the Convention. Furthermore, maintaining genetic diversity and the evolutionary processes that give rise to this diversity is fundamental to conservation planning and necessarily applied to genetically divergent subpopulations (Moritz, 2002). Moritz (2002) describes such sub-populations as evolutionary significant units (ESU).

The primary justification for treating *A. bidwillii* (Mt Lewis) separately from its congeners in the south arises from its unique genetics and independent evolutionary trajectory (Pye, 2005; Pye & Gadek, 2004).

Qualifying as an ESU (Pye & Gadek, 2004), and acknowledged by the IUCN as an important sub-population (Thomas, 2011), *A. bidwillii* (Mt Lewis) is undoubtedly in need of carefully considered conservation planning and management.

4.1.2 Red List Criteria & Methodologies

For a species (or other recognised taxonomic unit) to be considered threatened it must satisfy any one of five specific criteria that include: (A) past, present or projected population decline, (B) fragmented and limited geographic range, (C) small population size, fragmentation and observed decline, (D) very small population and restricted distribution, and (E) high risk of extinction (IUCN Standards & Petitions Committee, 2014). Depending on which of these criteria are met, a taxon may be classified as vulnerable (VU), endangered (EN) or critically endangered (CR) – the three threatened categories.

Population thresholds are applied to these criteria, which vary according to the rate of decline and quality of associated evidence. For example, criterion D has population thresholds (reproductively mature adults) at <50, <250, <1000 for CR, EN and VU respectively. However, where there is quantified evidence of a continuing population decline and the taxon meets criterion C above, these thresholds are higher (IUCN Standards and Petitions Subcommittee, 2014).

To confidently assign any of the criteria from A through to E requires a significant amount of data and quantified information. Data is considered to be low quality if it is inferred without quantifiable information. Capturing uncertainty through data quality ratings in this way ensures greater reliability of conservation assessments.

4.2 Methods

This conservation assessment of *A. bidwillii* (Mt Lewis) is based on the data and observations that I collected, and by the guidelines, criteria and strategic plans of the IUCN (2013; IUCN Red List Committee, 2013). Estimates of spatial distribution descriptors of the population, namely the extent of occurrence (EOO) and the area of occupancy (AOO) were determined using the Geospatial Conservation Assessment Tool (GeoCAT) (Kew Royal Botanic Gardens, 2015). The IUCN Red List conservation status assessment was determined using the IUCN's online assessment tool, the Species Information Service (SIS) Toolkit (IUCN, 2015).

GeoCAT is an open source geo-referenced tool, that performs a rapid analysis of the geographic range of a taxon consistent with the IUCN data requirements (Bachman et al., 2011).

Associate Supervisor Dr Charles Clarke provided access to the password protected training SIS Toolkit.

4.2.1 Extent of Occurrence and Area of Occupancy

EOO and AOO values and map (Figure 23) were generated in GeoCAT from field data and occurrence records obtained for chapters 2 and 3 of this study.

The EOO, described as the smallest possible area including all of the occurrence records, was 4 km^2. The AOO, which is the area within the EOO measured in grid squares measured 16 km^2, which is an anomaly generated by GeoCAT for species with very restricted ranges. In these instances the AOO is adjusted to match the EOO and in this case that is 4 km^2. They are presented in the methods as these values are prerequisite data for the conservation assessment.

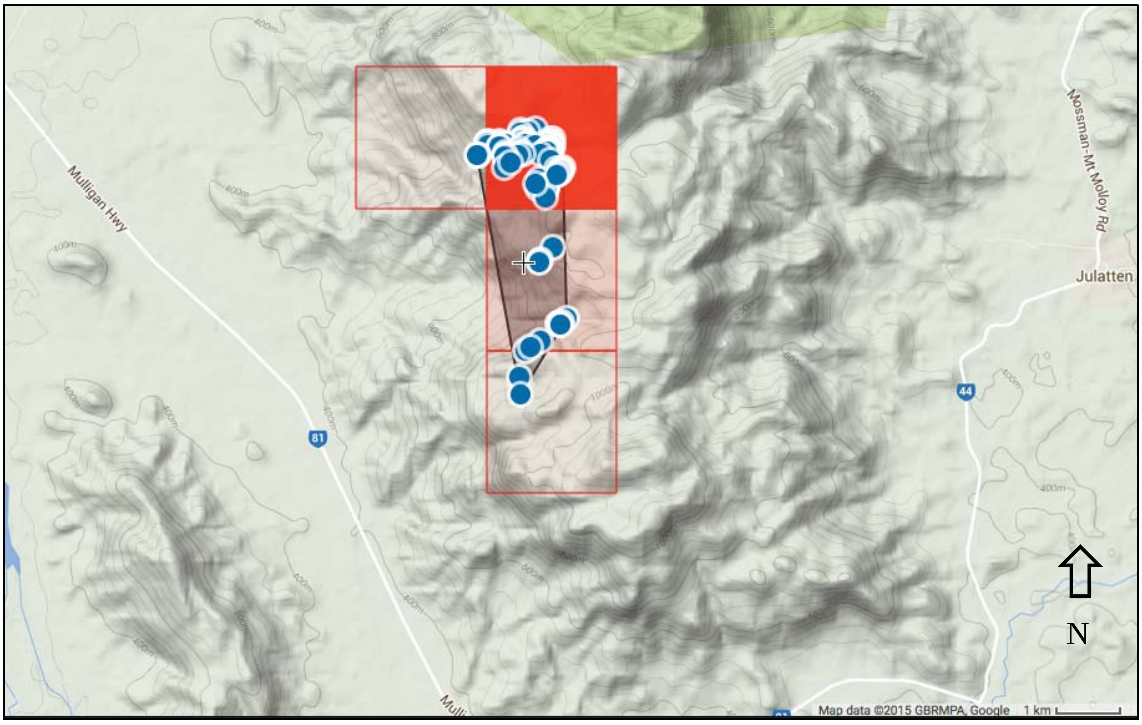


Figure 23. **GeoCAT output with the occurrence records for *A. bidwillii* in blue, AOO grid squares in red and the underlying EOO polygon.**

The EOO and AOO GeoCAT area values are then entered into the IUCN's (2015) SIS Toolkit. The additional qualifying statements and data fields included no observable decline and no extreme fluctuations for *A. bidwillii* (Mt Lewis) (author's obs.). However, the SIS Toolkit recognises the very restricted AOO of *A. bidwillii* and places it in a category prone to the impacts of human activity and stochastic events over the span of two generations. In the training run for this chapter we manually overrode this to avoid an assessment that does not appropriately consider the longevity of *A. bidwillii* (Mt Lewis), and its protection within the conservation estate.

4.2.2 Population

Reproductively mature trees of *A. bidwillii* (Mt Lewis) are thought to number between 100 (Thomas, 2011) and 400 (author's obs.). A total of 97 occurrence records were recorded for mature *A. bidwillii* (Mt Lewis) during this study. A total sample population of all size-classes including seedlings consisted of 806 individual plants.

The population data-fields also require information on observed stability, declines or fluctuations.

Again, while the population was thought to be stable with no declines or fluctuations, there is a suspected (less reliable than inferred) chance of a stochastic event such as a severe wildfire that may result in a population reduction of 50% of reproductively mature adults over a 100-year period. This in turn will lead to a reduction in the AOO. While this threat is unquantified, it is partly based on ecosystem changes expected over the next 75 years as a result of climate change. These expectations include a catastrophic increase in temperatures in some areas (Reside et al., 2013).

4.2.3 Habitats and Ecology

Two habitat types, or biomes, were listed for *A. bidwillii* (Mt Lewis) in the limited options provided in the SIS Toolkit. These were rainforest and 'other' to recognise *A. bidwillii* (Mt Lewis) occurrences in tall open forest.

No decline in extent, area or quality of habitat was entered into the SIS Toolkit. Justification is that the habitat is within the Wet Tropics World Heritage Area and the Brooklyn Sanctuary Nature Refuge. The primary land use is conservation and the entire population of *A. bidwillii* (Mt Lewis) is within the protected area estate. This was also noted for other data fields.

4.2.4 Life History

There is no published research into the age of *A. bidwillii* throughout its range. *A. cunninghamii* has been documented at 320 years in age (Ogden, 1981) while *A. araucana* can exceed 1000 years in age (Burns, 1993).

Minimum age at maturity was set at 30 years on the observation of cone bearing trees with 20cm DBH. However, this assumes an environment conducive of continuous growth without impediments.

4.2.5 Threats

There are five broad threats likely to have an impact on *A. bidwillii* (Mt Lewis). Fire and genetic outbreeding depression are already recognised by the IUCN for *A. bidwillii* (Mt Lewis) (Thomas, 2011). Increased extremes of fire risk, drought and cyclone severity are anticipated to increase over the next 75 years as a result of climate change, with resultant impacts on biodiversity (Reside et al., 2013).

In addition, the introduced *Lantana camara,* a weed of national significance, and the invasive *Rubus alceifolius* are present within the areas supporting *A. bidwillii* (author's obs.). Together, both species can impede the natural recruitment of trees and shrubs where they occur in the Wet Tropics (Werren, 2001).

4.3 Results

Based on the data and descriptive information entered, the IUCN's (2015) training SIS Toolkit identifies *A. bidwillii* (Mt Lewis) as vulnerable (VU D2ce D).

Specifically *A. bidwillii* (Mt Lewis) is vulnerable (VU) with a very restricted area of occupancy with a set of plausible future threats that could drive the taxon towards extinction over time (D2) resulting in a decline in AOO, EOO (4km^2) or habitat quality (c), impacted by introduced taxa and pathogens (e) and with a very small and restricted number of reproductively mature individuals (D). Definitions are according to the IUCN Standards and Petitions Subcommittee (2014).

4.4 Discussion

Listed as least concern, the Mount Lewis subpopulation of *A. bidwillii* is unlikely to receive the conservation management and planning it deserves. Assessing its conservation status in isolation of populations elsewhere is intended to highlight the precarious nature of this sub-population's existence. In addition, Pye (2005) recommended the subpopulation be considered independently of the southern populations.

In any case, assigning vulnerable status to *A. bidwillii* (Mt Lewis) seems an uncontroversial, if not conservative, conclusion. The SIS toolkit was populated with both quantified data and inferred observations and a more robust approach may elevate the status to endangered. For comparison, the rare *Prumnopitys ladei* (Podocarpaceae), which also occurs near Mount Lewis, is listed as vulnerable by the IUCN (Farjon, 2013). *P. ladei* has a slightly bigger distribution but is effectively confined to upland rainforest at Mount Lewis and Mount Spurgeon, is in a more stable environment and is assumed to have a greater number (<1000) of mature individuals.

The longevity of *A. bidwillii* remains unknown and this hinders understanding of temporal responses to disturbance and the long-term risk of threats. Age estimates of *A. cunninghamii* on the Atherton Tableland with a DBH of 120cm are thought to be around 300 years old (Ogden, 1981) while *A. araucana* from South America, is known to reach an age >1000 years (Burns, 1993). The age of the largest *A. bidwillii* at Mount Lewis observed during this study (Figure 24) could be anywhere between 300 and 1000 years.

Figure 24. The largest tree recorded in this study (Site A) measured 144cm DBH is most likely >300 years old.

This tree may also have established when the forest was more open and dominated by *E. grandis* which it has outlived and now exists as a >50m high emergent in rainforest

Fire is perhaps one of the most complex and immediately important threats. The impact of fire on Australia’s Araucariaceae is little studied and largely restricted to analysis of fossil pollen records where increasing aridity and fire are thought to have caused the retreat of once widespread Araucarian forests (Kershaw & Wagstaff, 2001; Moss & Kershaw, 2000).

Pye and Gadek (2004) noted that fire associated with weather cycles during the Quaternary period are likely to have had the most influence on population size and distribution of *A. bidwillii* in Australia. Further, the current fragmentation, distribution and population size of *A. bidwillii* in Queensland is likely to have arisen from climate variability and increased fire of the Holocene (Pye & Gadek, 2004).

However, fire can play both a restorative and destructive role in the ecology of many conifers, particularly in the southern hemisphere. Examples include *A. araucana* in Chile (Burns, 1993; Gonzalez et al., 2010), *Lagarostrobos franklinii* in Tasmania (Gibson & Brown, 1991), *Callitris* spp. across inland Australia (Cohn et al., 2011), and most Araucariaceae and other conifers in New Caledonia (Jaffré et al., 2010; Kettle et al., 2012; Perry & Enright, 2004).

Pye (2005) provides anecdotal observations of fire killed *A. bidwillii* (Mt Lewis) seedlings at Mount Lewis while also suggesting thicker bark on mature trees provides some form of protection. Pye (2005) also speculates that fire, timed with a seed masting event, could be conducive to a recruitment cohort of *A. bidwillii* but there has not been any published research on this.

Complex interactions of environmental and abiotic factors undoubtedly influence the occurrence, persistence and abundance of *A. bidwillii* (Mt Lewis). Occurring in both pyrophobic rainforest, pyrophytic tall open forest (as described by Warmen and Moles (2009)) and through the ecotonal gradient of the two vegetation types, *A. bidwillii* (Mt Lewis) may rely on the ongoing interaction of these two communities for critical phases of its lifecycle.

Tall open forest dominated by *E. grandis* in the Australian Wet Tropics occupies a narrow niche primarily along the western edge of rainforests (Turton & Sexton, 1996). In many places, rainforest is expanding into tall open forest (Tng et al., 2011) with the latter considered to be under threat from this expansion (Hopkins et al., 1996). This is generally considered to be the case at AWC's Brooklyn Sanctuary and the forest within the study area (Stanton et al., 2013).

Alternatively, tall open forests including those dominated by *E. grandis,* are thought to be pseudo-stable and ecotonal, naturally shifting with an expanding rainforest margin over generations (Warman & Moles, 2009). Furthermore, Tng et al., (2012) suggests that tall eucalypts are more closely affiliated with rainforest trees in functional traits and that their ecology is intertwined with rainforests, similar to the mixed temperate rainforest with emergent eucalypts in Tasmania and Victoria.

The primary intention of prescribed burning every 3 to 10 years in tall open forest as recommended by the Queensland Government (2014) is to cause mortality of rainforest species and trigger open forest recruitment. Based on anecdotal observations and comparison with other Araucariaceae, prescribed burning will potentially cause the mortality of some size-class or age-classes of *A. bidwillii* (Mt Lewis) with unknown implications for the population over time. Additionally, without the occurrence of tall open forest along the western margin of rainforest, recruitment opportunities for *A. bidwillii* (Mt Lewis) will diminish.

However, in the absence of fire and at the rate of change of continued rainforest expansion, 85% of tall open forest would remain after 100 years. Furthermore, it would take 2000 years before 75% of the current extent of tall open forest would be engulfed by rainforest (Tng et al., 2011). Over that period of time, Tng et al. (2011) suggest it is almost certain that cyclones, droughts and landscape fires will push back the rainforest expansion, returning the cycle to an early succession phase allowing for the recruitment of *E. grandis.* If this scenario unfolded at Mount Lewis, recruitment would potentially include *A. bidwillii,* such a scenario is consistent with Ogden and Stewart's (1995) temporal stand replacement model.

The population structures explored in Chapter 3 and the potentially suitable habitat identified in Chapter 2 demonstrate that *A. bidwillii* (Mt Lewis) is not restricted to either tall open forest or rainforest. Although more research is required, it may be dependent on the interaction of the two communities and their ongoing expansion and contraction over many generations, perhaps over several hundred years.

If we consider *A. bidwillii* (Mt Lewis) to be worthy of dedicated conservation planning and management, facilitating recruitment and persistence across the rainforest – tall open forest ecotone is essential.

5. Conclusions

In this thesis I have presented new information on the habitat, distribution, population structure and conservation status of the Mount Lewis subpopulation of *A. bidwillii.* In addressing the first aim through the use of species distribution modelling (Chapter 2) I have established that there are additional areas of high habitat suitability adjacent to the known occurrences of *A. bidwillii* at Mount Lewis. Further the subpopulation appears strongly associated with the margins of tall open forest and rainforest where it occurs on the western draining sub-catchments of the Carbine Tableland. This is clearly demonstrated through both the species distribution modelling in Chapter 2 and the population data in Chapter 3.

Figure 25. Emergent *A. bidwillii* in simple notohpyll vine forest in Leichhardt Creek catchment, Mount Lewis.

The second aim of this thesis was to address the question of recruitment through an investigation of the population structure of *A. bidwillii* at Mount Lewis (Chapter 3). I investigated two broad strategies of recruitment and mortality by investigating the suitability of models that assume continuous recruitment and those that infer episodic recruitment in response to disturbance. While evidence of recruitment was observed, it did not conform to the expectations of the negative exponential model, lacking a constant rate of mortality. Differences between the population structure of *A. bidwillii* in tall open forest and rainforest suggest that there may be an interaction between vegetation type and the distribution of size-class which was confirmed using a linear model. I found that tall open forest supported a significantly greater abundance of seedlings, saplings and smaller trees of *A. bidwillii* than did rainforest. In addition rainforest supported the largest and presumably oldest, and often emergent, trees (Figure 25) and very few smaller size-classes. Recruitment of *A. bidwillii* within rainforest cannot be assumed and complex and long-term temporal interactions of ecotone dynamics may be enabling the persistence of *A. bidwillii* within the study area.

In addressing the third aim (Chapter 4) I establish that the Mount Lewis sub-population of *A. bidwillii* meets the criteria for listing as vulnerable under the International Union for the Conservation of Nature (IUCN) categories and criteria. Notwithstanding the eligibility of the subpopulation to be officially listed, the intent of this chapter was to highlight the population’s precarious existence and focus conservation and management attention on the stands.

5.1 Recommendations

The management and conservation of the Mount Lewis subpopulation of *A. bidwillii* is critical for the management of the species as a whole (Pye, 2005). Responding to new information on the abundance, habitat and population structures in this thesis necessitates a review of how the landscape supporting the Mount Lewis subpopulation of *A. bidwillii* is managed.

Distribution

The known extent of *A. bidwillii* increased as a result of survey effort for this research. This was primarily in Leichhardt Creek catchment. It is likely that further survey effort would reveal a greater extent in Station Creek immediately adjacent to the south where the other known stands occur. Assisted by the distribution modelling in Chapter 2 further survey effort for *A. bidwillii* should be undertaken in areas with a high Habitat Suitability Value (HSV) identified in Chapter 2 along the western escapement of the Carbine Tableland and restricted to areas south of the McLeod River. In addition, Bakers Blue Mountain, the closest adjacent areas to Mount Lewis, was also identified as an area of high HSV. Strategic aerial surveys over targeted locations will most likely yield the best results and should be considered as a management priority. Results will help to confirm area of occupancy and extent of occurrence.

The subpopulation in Wooroonooran National Park at Cannabullen Falls is in need of monitoring and management. Virtually nothing is known about the population structure and numbers of mature trees.

Fire

Fire regimes may be an important contributing factor determining either the extinction or persistence of *A. bidwillii* in the landscape, the role of fire in tall open forest of Australia’s Wet Tropics remains unresolved and contested. Some authors suggest management interventions are interrupting natural ecological processes that operate over hundreds of years (Tng et al., 2012). Others authors suggest that regular fire on a short rotation is necessary to prevent tall open forest from becoming extinct (Stanton et al., 2014).

However, long-term temporal processes influencing vegetation structure and dynamics, such as those affecting the tall open forest and rainforest of Leichhardt Creek catchment have potentially facilitated the persistence of *A. bidwillii* within the landscape. Fire every three to ten years that causes the mortality of rainforest species is likely to have an adverse impact on *A. bidwillii* seedlings, saplings and juvenile trees. This will likely diminish the opportunities for *A. bidwillii* to attain reproductive maturity in tall open forest. The practice of burning on short rotations within tall open forest may need reviewing at specific locations if our objective is to maximise the survivorship of *A. bidwillii* and allow for a natural increase in the population over time.

Therefore, it is recommended that areas of tall open forest known to support *A. bidwillii* are quarantined from prescribed burning at least until there is robust evidence on the species’ response to fire.

Mapping

Regional Ecosystem vegetation mapping currently identifies six small and discrete polygons of RE 7.12.16c (simple notophyll vine forest with emergent *Araucaria*) (pink polygons in Figure 26). The extent of this vegetation type is more extensive and contiguous than is currently mapped as indicated by additional records (black dots) in Figure 26. Official vegetation mapping by the Queensland Government should be updated to reflect the greater extent of *A. bidwillii* within RE 7.12.16c. In addition, some consideration should be given to mapping tall open forest known to support *A. bidwillii* especially as it warrants a differing management approach that other similar tall open forest.

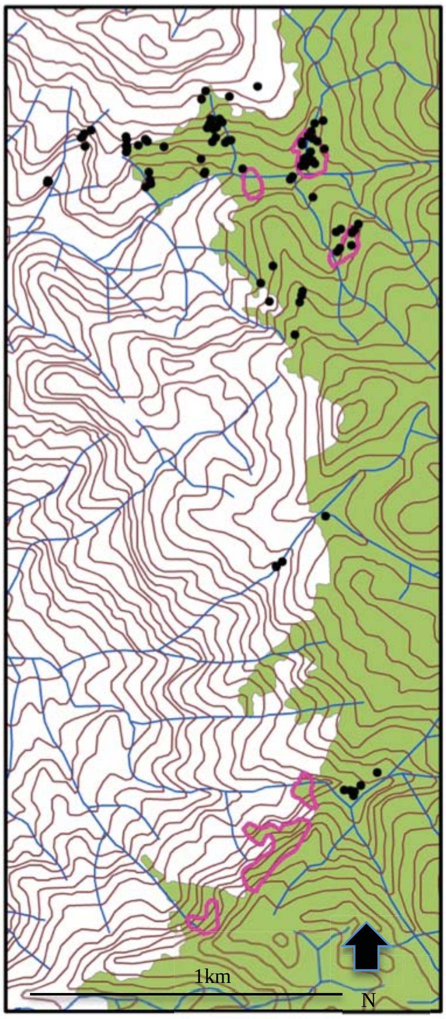


Figure 26. **Additional areas of *A. bidwillii* recorded for this study increase the area of known notohpyll vine forest with emergent *Araucaria* in Leichhardt Creek**

Conservation Status

I consider the Mount Lewis population of *A. bidwillii* to be eligible for consideration under the IUCN’s criteria for listing as a threatened taxon because it is genetically distinct, qualifies as an ESU, represents a unique and isolated subpopulation (at the northern extremity of the taxon’s range) and is exposed to unique threats not faced by other subpopulations. I also present the case that the Mount Lewis subpopulation of *A. bidwillii* meets the relevant criteria for listing as vulnerable and, as Pye proposed in 2005, in need of its own conservation management and planning.

6. References

Accad, A. (1999). *Wet Tropics 80-m Digital Elevation Model*. Cairns: Wet Tropics Management Authority. .

Ahmed, M, & Ogden, J. (1987). Population dynamics of the emergent conifer *Agathis australis* (D. Don) Lindl. (kauri) in New Zealand I. Population structures and tree growth rates in mature stands. *New Zealand Journal of Botany, 25*, 217-229.

Aiba, S, Hanya, G , Tsujino, R, Takyu, M , Seino, T , Kimura, K, & Kitayama, K. (2007). Comparative study of additive basal area of conifers in forest ecosystems along elevational gradients *Ecological Restoration*(22), 439-450.

Bachman, S, Moat, J, Hill, AW, de Torre, J, & Scott, B. (2011). Supporting Red List threat assessments with GeoCAT: geospatial conservation assessment tool. *Zookeys*(150), 117-126.

Begon, M, Townsend, CR, & Harper, JL. (2006). *Ecology: from individuals to ecosystems* Melbourne Blackwell Publishing

Biffin, E, Hill, RS, & Lowe, AJ. (2010). Did kauri (*Agathis*: Araucariaceae) really survive the Oligocene drowning of New Zealand? *Systematic Biology, 59*(5), 594-602.

Blake, T. (2002). 'This nobel tree': J.C. Bidwill and the naming of the bunya pine. *On the Bunya Trail: Queensland Review Special Edition, 9*(2), 39-46.

Boland, DJ, Brooker, MIH, Chippendale, GM, Hall, N, Hayland, BPM, Johnston, RD, Kleining, DA, McDonald, MW, & Turner, JD. (2006). *Forest Trees of Australia* Melbourne: CSIRO.

Bond, WJ. (1989). The tortoise and the hare: ecology of angiosperm dominance and gymnosperm persistence. *Biological Journal of the Linnean Society, 36*, 227-249.

Brodribb, TJ, Holbrook, NM, & Hill, RS. (2005). Seedling growth in conifers and angiosperms: impacts of contrasting xylem structure. *Australian Journal of Botany, 53*, 749-755.

Brodribb, TJ, Pitterman, J, & Coomes, DA. (2012). Elegance versus speed: examining the competition between conifer and angiosperm trees. *International Journal of Plant Sciences, 173*(6), 673-694.

Burnham, KP, & Anderson, DR. (2002). *Model selection and multimodel inference : a practical information-theoretic approach*. USA: Springer.

Burns, BR. (1993). Fire-induced dynamics of *Araucaria araucana-Nothofagus antarctica* forest in the southern Andes. *Journal of Biogeography, 20*(6), 669-685.

Burrows, GE, & Stockey, RA. (1994). The developmental anatomy of cryptogeal germination in Bunya Pine (*Araucaria bidwillii*). *International Journal of Plant Sciences, 155*(5), 519-537.

Cantrill, DJ (1992). Araucarian foliage from the lower Cretaceous of southern Victoria, Australia. *International Journal of Plant Sciences, 153*(4), 622-645.

Ceballos, G, Ehrlich, PR , Barnosky, AD , García, A, Pringle, RM , & Palmer, TM (2015). Accelerated modern human–induced species losses: entering the sixth mass extinction. *Science Advances, 1*(5), e1400253.

Clark, DB, & Clark, DA. (1995). Abundance, growth and mortality of very large trees in neotropical rain forest,. *Forest Ecology and Management., 80*, 235-244.

Cohn, JS, Lunt, ID, Ross, KA, & Bradstock, RA. (2011). How do slow-growing, fire-sensitive conifers survive in flammable eucalypt woodlands? *Journal of Vegetation Science, 22*, 425-435.

Condit, R, Sukumar, R, Hubbell, SP, & Foster, RB. (1998). Predicting population trends from size distributions: a direct test in a tropical tree community. *The American Naturalist, 152*(4), 495-509.

Costion, CM, Simpson, L, Pert, PL, Carlsen, MN, Kress, WJ, & Crayn, D. (2015). Will tropical mountaintop plant species survive climate change? Identifying key knowledge gaps using species distribution modelling in Australia *Biological Conservation, 191*, 322-330.

Cropper, SC. (1993). *Management of Endangered Plants* Melbourne CSIRO.

Cullen, PJ. (1987). Regeneration patterns in populations of *Athrotaxis selaginoides* D. Don. from Tasmania. *Journal of Biogeography, 14*(1), 39-51.

Elith, J, Phillips, SJ, Hastie, T, Dudik, M, Chee, YE, & Yates, CJ. (2011). A statistical explanation of MaxEnt for ecologists,. *Diversity and Distributions, 17*, 43-57.

Enright, NJ. (1982a). The ecology of Araucaria species in New Guinea. I. Ordination studies of forest types and environments. *Australian Journal of Ecology, 7*, 23-38.

Enright, NJ. (1982b). The ecology of Araucaria species in New Guinea. II. Pattern in the distribution of young and mature individuals and light requirements of seedlings. *Australian Journal of Ecology, 7*, 39-48.

Enright, NJ. (1982c). The ecology of Araucaria species in New Guinea. III. Population dynamics of sample stands. *Australian Journal of Ecology, 7*, 227-237.

Enright, NJ. (1995). Conifers of tropical Australasia. In N. Enright & R. Hill (Eds.), *Ecology of the Southern Conifers* Melbourne Melbourne University Press

Enright, NJ, & Goldblum, D. (1998). Stand structure of the emergent conifer *Agathis ovata* in forest and maquis, Province Sud, New Caledonia *Journal of Biogeography, 25*, 641-648.

Enright, NJ, & Hill, RS. (1995). *Ecology of the Southern Conifers* (N. Enright & R. Hill Eds.). Melbourne Melbourne University Press

Enright, NJ, Hill, RS, & Veblen, TT. (1995). The southern conifers - an introduction. In N. Enright & R. Hill (Eds.), *Ecology of the Southern Conifers* Melbourne Melbourne University Press

Enright, NJ, & Ogden, J. (1995). The southern conifers - a synthesis In N. Enright & R. Hill (Eds.), *Ecology of the Southern Conifers*. Melbourne: Melbourne University Press.

Enright, NJ, Ogden, J, & Rigg, LS. (1999). Dynamics of forests with Araucariaceae in the western Pacific *Journal of Vegetation Science, 10*(6), 793-804.

Farjon, A. (2013). *Prumnopitys ladei. The IUCN Red List of Threatened Spcies 2013.* Retrieved 2015

Finckh, M, & Paulsch, A. (1995). The ecological strategy of *Araucaria araucana*. *Flora, 190*, 365-382.

Flannery, T. (2012). After the future: Australia's new extinction crisis. *Quarterly Essay, 48*, 1-80.

Franklin, J. (2010). *Mapping Species Distributions: spatial inference and prediction.* Cambridge, UK: Cambridge University Press.

Gibson, N, & Brown, MJ. (1991). The ecology of *Lagarostrobos franklinii* (Hook.f.) Quinn (Podocarpaceae) in Tasmania. 2. Population structure and spatial pattern. *Australian Journal of Ecology*(6), 223-229.

Gonzalez, ME, Veblen, TT, & Sibold, JS. (2010). Influence of fire severity on stand development of *Araucaria araucana-Nothofagus pumilio* stands in the Andean cordillera of south-central Chile. *Austral Ecology, 35*, 597-615.

Graham, CH, VanDerWal, J, Phillips, SJ, Moritz, C, & Williams, SE. (2010). Dynamic refugia and species persistence: tracking spatial shifts in habitat through time. *Ecography, 33*, 1062-1069.

Gray, B. (1975). Size-composition and regeneration of *Araucaria* stands in New Guinea. *The Journal of Ecology, 63*(1), 273-289.

Guisan, A, & Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecology Letters, 8*, 993-1009.

Guisan, A, & Zimmermann, NE. (2000). Predictive habitat distribution models in ecology. *Ecological Modelling, 135*, 147-186.

Haebich, A. (2002). Editorial *On the Bunya Trail: Queensland Review Special Edition, 9*(2), vii-xi.

Harrington, GN, Thomas, MR, Bradford, MG, Sanderson, KD, & Irvine, AK. (2000). Structure and plant species dominance in North Queensland wet sclerophyll forests. *Proceedings of the Royal Society of Queensland, 109*, 59-74.

Havel, JJ. (1971). The Araucaria forests of New Guinea and their regenerative capacity. *The Journal of Ecology, 59*(1), 203-214.

Hernandez-Castillo, GR, & Stocky, RA. (2002). Palaeobotany of the Bunya Pine. *On the Bunya Trail: Queensland Review Special Edition, 9*(2).

Hett, JM, & Loucks, OL. (1976). Age Structure Models of Balsam Fir and Eastern Hemlock. *The Journal of Ecology, 64*(3), 1029-1044.

Hill, KD. (1998). Pinophyta, Araucariaceae *Flora of Australia: ferns gymnosperms and allied groups* (Vol. 48, pp. pp. 563-569). Melbourne: CSIRO.

Hill, RS, & Brodribb, TJ. (1999). Southern conifers in time and space. *Australian Journal of Botany, 47*, 639-696.

Hill, RS, & Scriven, LJ. (1998). The fossil record of conifers in Australia. *Flora of Australia* (Vol. 48, pp. pp. 527-538). Melbourne: CSIRO.

Hill, RS, Truswell, EM, McLoughlin, S, & Dettman, ME. (2000). Evolution of the Australian flora: fossil evidence *Flora of Australia* (Vol. 1, pp. pp. 225-302). Melbourne CSIRO.

Hitimana, J, Kiyiapi, JL, & Njunge, JT. (2004). Forest structure characteristics in disturbed and undisturbed sites of Mt. Elgon Moist Lower Montane Forest, western Kenya. *Forest Ecology and Management., 194*, 269-291.

Hopkins, MS, Head, J, Ash, JE, Hewett, RK, & Graham, AW. (1996). Evidence of a Holocene and continuing recent expansion of lowland rain forest in humid, tropical North Queensland. *Journal of Biogeography., 23*, 737-745.

Hörnberg, G, Ohlson, M, & Zackrisson, O. (1995). Stand Dynamics, Regeneration Patterns and Long-Term Continuity in Boreal Old-Growth Picea abies Swamp-Forests. *Journal of Vegetation Science, 6*(2), 291-298.

Hufkens, K, Scheunders, P, & Ceulemans, R. (2008). Ecotones in vegetation ecology: methodologies and definitions revisited. *Ecological Research, 24*(5), 977-986.

Huth, J. (2002). Introducing the Bunya Pine - nobel denizen of the scrub. *On the Bunya Trail: Queensland Review Special Edition, 9*(2), 7-20.

Hyland, BPM, Whiffen, T, Christophel, DC, Gray, B, & Elick, RW. (2003). *Australian Tropical Rainforest Plants: trees shrubs and vines*.

IUCN. (2013). Documentation standards and consistency checks for IUCN Red List assessments and species accounts. Version 2. In I. R. L. C. a. I. S. S. Committee (Ed.). http://www.iucnredlist.org/documents/RL_Standards_Consistency.pdf.

IUCN. (2015). Species Information Service (SIS) Toolkit, rev. 2.0. https://train.iucnsis.org/apps/org.iucn.sis.server/SIS/index.html

IUCN Red List Committee. (2013). The IUCN Red List of Threatened Species™ Strategic Plan 2013 - 2020. Version 1.0.: IUCN Red List Committee.

IUCN Standards and Petitions Subcommittee. (2014). Guidelines for Using the IUCN Red List Categories and Criteria. Version 11. In P. b. t. S. a. P. Subcommittee (Ed.). http://www.iucnredlist.org/documents/RedListGuidelines.pdf.: IUCN.

Ives, AR. (2015). For testing the significance of regression coefficients, go ahead and log-transform count data. *Methods in Ecology and Evolution, 6*, 825-835.

Jaffré, T, Munzinger, J , & Lowry II, PP. (2010). Threats to the conifer species found on New Caledonia’s ultramafic massifs and proposals for urgently needed measures to improve their protection. *Biodiversity and Conservation, 19*(5), 1485-1502.

Jerome, P. (2002). Boobarran Ngummin: the Bunya Mountains. *On the Bunya Trail: Queensland Review Special Edition, 9*(2), 1-6.

Johnston, M, & Gillman, M. (1995). Tree population studies in low-diversity forests, Guyana. 1. Floristic composition and stand structure. *Biodiversity and Conservation, 4*, 339-362.

Kelly, CK, Smith, HB, Buckley, YM, Carter, R, Franco, M, Johnson, W, Jones, T, May, B, Ishiwara, RP, Perez-Jimennez, A, Magallanes, AS, Steers, H, & Waterman, C. (2001). Investigations in commonness and rarity: a comparative analysis of co-occurring, congeneric Mexican trees. *Ecology Letters, 4*, 618-627.

Kershaw, AP, Bretherton, SC, & van der Kaars, S (2007). A complete pollen record of the last 230 ka from Lynch's Crater, northeastern Australia. . *Palaeogeography, Palaeoclimatology, Palaeoecology, 151*, 23-45.

Kershaw, AP, & McGlone, MS (1995). The Quaternary history of the southern conifers. In N. Enright & R. Hill (Eds.), *Ecology of the Southern Conifers* (pp. 30-63). Melbourne: Melbourne University Press

Kershaw, AP, & Wagstaff, B. (2001). The southern conifer family Araucariaceae: history, status and value for paleoenvironmental reconstruction. . *Annual Review of Ecology and Systematics, 32*(2001), 397-414.

Kettle, CJ, Ennos, RA, Jaffre, T, McCoy, S, Borgne, TL, Gardner, M, & Hollingsworth, PM. (2012). Importance of demography and dispersal for the resilience and restoration of a critically endangered tropical conifer Araucaria nemorosa. *Diversity and Distributions, 18*, 248-249.

Kew Royal Botanic Gardens. (2015). GeoCAT: Geospatial Conservation Assessment Tool. Retrieved 2015, from Kew Gardens

Kohira, M, & Ninomiya, I. (2003). Detecting tree populations at risk for forest conservation management: using single-year vs. long-term inventory data,. *Forest Ecology and Management.*(174), 423-435.

Leak, WB. (1965). The J-shaped probability distribution *Forest Science, 11*(4), 405-409.

Lidgard, S, & Crane, PR. (1988). Quantitative abalysis of the early angiosperm radiation *Nature, 331*, 344-346.

McCarthy, JW, & Weetman, G. (2006). Age and size structure of gap-dynamic, old-growth Boreal forest stands in Newfoundland. *Silva Fennica, 40*(2), 209-230.

Merow, C, Smith, MJ, & Silander, JA, Jr. (2013). A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography*(36), 1058-1069.

Moritz, C. (2002). Strategies to protect biological diversity and the evolutionary processes that sustain it. *Systematic Biology, 51*(2), 238-254.

Moss, PT, & Kershaw, AP. (2000). The last glacial cycle from the humid tropics of northeastern Australia: comparison of a terrestrial and marine record. *Palaeogeography, Palaeoclimatology, Palaeoecology, 155*, 155-179.

Natural Resource Management Ministerial Council. (2010). *Australia's Biodiversity Conservation Strategy 2010-2030*. Canberra Australian Government.

Neldner, VJ, Niehus, RE, Wilson, BA, McDonald, WJF, & Ford, AJ. (2015). The Vegetation of Queensland: Descriptions of Broad Vegetation Groups, Version 2.0. Queensland Herbarium Department of Science, Information Technology and Innovation.

Newton, AC. (2007). *Forest Ecology and Conservation.* Oxford Oxford University Press.

Nix, H. (1991). Biogeography: pattern and process. In H. Nix & S. MA (Eds.), *Rainforest Animals, Atlas of Vertebrates Endemic to Australia's Wet Tropics* Canberra: Australian National Parks and Wildlife Service, Commonwealth of Australia

Ogden, J. (1981). Dendrochronological studies and the determination of tree ages in the Australian tropics. *Journal of Biogeography, 8*(5), 405-420.

Ogden, J. (1985). An introduction to plant demography with special reference to New Zealand trees. *New Zealand Journal of Botany, 23*(751-772).

Ogden, J, & Stewart, GH. (1995). Community dynamics of the New Zealand conifers. In N. Enright & R. Hill (Eds.), *Ecology of the Southern Conifers*. Melbourne Melbourne University Press

Ogden, J, Wardle, GM, & Ahmed, M. (1987). Population dynamics of the emergent conifer *Agathis australis* (D. Don) Lindl. (kauri) in New Zealand II. Seedling population sizes and gap-phase regeneration. *New Zealand Journal of Botany, 25*, 231-242.

Oliveira-Filho, AT, Camisao-Neto, AA, & Volpato, MML. (1996). Structure and dispersion of four tree populations in an area of montane semideciduous forest in southeastern Brazil. *Biotropica, 28*(4), 762-769.

Peres, CA, & Baider, C. (1997). Seed dispersal, spatial distribution and population structure of Brazil nut trees (Bertholletia excelsa) in Southeastern Amazonia. *Journal of Tropical Ecology, 13*(4), 595-616.

Perry, GLW, & Enright, NJ. (2004). Spatial modelling of "alternative" future landscapes under climate change and fire suppression, Mont Do New Caledonia *Pacific Conservation Biology, 9*, 248-264.

Phillips, SJ, Anderson, RP, & Schapire, RE. (2006). Maximum entropy modelling of species geographic distributions *Ecological Modelling, 190*, 231-259.

Phillips, SJ, & Dudik, M. (2008). Modelling of species distributions with Maxent: new extensions and comprehensive evaluation. . *Ecography, 31*, 161-175.

Pye, MG. (2005). *Gentetic diversity and divergence within and among natural populations of Araucaria in eastern Australia.* (PhD), James Cook University

Pye, MG, & Gadek, PA. (2004). Genetic diversity, differentiation and conservation in *Araucaria bidwillii* (Araucariaceae), Australia's Bunya Pine. *Conservation Genetics, 5*, 619-629.

Queensland Government. (2014). Regional Ecosystems descriptions. 2015

Queensland Government. (2015). Queensland Globe. 2015, from https://http://www.business.qld.gov.au/business/support-tools-grants/services/mapping-data-imagery/queensland-globe

R Development Core Team. (2012). R: A Language and Environment for Statistical Computing. Vienna, Austria R Foundation for Statistical Computing

Reside, AE, VanDerWal, J, Phillips, BL, Shoo, LP, Rosauer, DF, Anderson, BJ, Welbergen, JA, Moritz, C, Ferrier, S, Harwood, TD, Williams, KJ, Mackey, B, Hugh, S, & Williams, SE &YM. (2013). Climate change refugia for terrestrial biodiversity: Defining areas that promote species persistence and ecosystem resilience in the face of global climate change (pp. 216 pp.). Gold Coast National Climate Change Adaptation Research Facility.

Rigg, LS, Enright, NJ, & Jaffre, T. (1998). Stand structure of the emergent conifer *Araucaria laubenfelsii* in maquis and rainforest, Mont Do, New Caledonia. *Australian Journal of Ecology, 23*, 528-538.

Rigg, LS, Enright, NJ, Jaffre, T, & Perry, GLW. (2010). Contrasting population dynamics of the endemic New Caledonian conifer *Araucaria laubenfelsii* in maquis and rain forest. *Biotropica, 42*(4), 479-487.

Rochester, WA. (2003). Environmental attribute surfaces for the Wet Tropics bioregion

Setoguchi, H, Osawa, TA, Pintaud, JC, Jaffrey, T, & Veillon, JM. (1998). Phylogenetic relationships within Araucariaceae based on rbc*L* gene sequences. *American Journal of Botany, 85*(11), 1507-1516.

Silva, LCR, & Anand, M. (2011). Mechanisms of Araucaria (Atlantic) forest expansion into southern Brazilian grasslands. *Ecosystems, 14*(8), 1354-1371.

Singer, RJ, & Burgman, MA. (1999). The regeneration ecology of *Kunzea ericoides* (A. Rich.) J. Thompson at Coranderrk Reserve, Healesville *Australian Journal of Ecology, 24*, 18-24.

Smith, IR, & Butler, D. (2002). The Bunya in Queensland's Forests. *On the Bunya Trail: Queensland Review Special Edition, 9*(2), 31-39.

Smith, IR, & Butler, D. (2009). *The Bunya Pine: the ecology of Australia's other living fossil Araucarian.* . Paper presented at the 2002 International Araucariaceae Symposium, Dandabah Area-Bunya Mountains South East Queensland, Australia.

Souza, AF. (2007). Ecological interpretation of multiple population size structures in trees: The case of Araucaria angustifolia in South America. *Austral Ecology, 32*, 524-533.

Stanton, P, Jensen, R, & Webb, T. (2013). Vegetation Mapping of Brooklyn Sanctuary: Australian Wildlife Conservancy

Stanton, P, Stanton, D, Stott, M, & Parsons, M. (2014). Fire exclusion and the changing landscape of Queensland's Wet Tropics Bioregion 1. The extent and pattern of transition. *Australian Forestry, 77*(1), 51-57.

Stocky, RA. (1975). Seeds and embryos of *Araucaria mirabilis*. *American Journal of Botany, 62*, 856-868.

Stocky, RA. (1982). The Araucariaceae: an evolutionary perspective. . *Review of Palaeobotany and Palynology, 37*(1982), 133-154.

Swets, JA. (1988). Measuring the accuracy of diagnostic systems *Science, 240*, 1285-1293.

Thomas, P. (2011). *Araucaria bidwillii The IUCN Red List of Threatened Species* Version 2014.3. Retrieved 30 May 2015, from http://www.iucnredlist.org/details/42195/0

Tindale, NB. (1974). *Aboriginal Tribes of Australia, Their Terrain, Environmental Controls, Distribution, Limits and Proper Names* Canberra: Australian National University Press.

Tittensor, DP, Baco, AR, Brewin, PE, Clark, MR, Consalvey, M, Hall-Spencer, J, Rowden, AA, Schlacher, T, Stocks, KI, & Rogers, AD. (2009). Predicting global habitat suitability for stony corals on seamounts. . *Journal of Biogeography, 36*(6), 1111-1128.

Tng, DYP, Murphy, BP, Weber, E, Sanders, G, Williamson, GJ, Kemp, J, & Bowman, DMJS. (2011). Humid tropical rain forest has expanded into eucalypt forest and savanna over the last 50 years. *Ecology and Evolution, 2*(1), 34-45.

Tng, DYP, Williamson, GJ, Jordan, GJ, & Bowman, DMJS. (2012). Giant eucalypts - globally unique fire-adapted rain-forest trees? *New Phytologist, 196*, 1001-1014.

Tracey, GJ. (1982). *The Vegetation of the Humid Tropical Region of North Queensland.* Melbourne: CSIRO.

Turton, SM, & Sexton, GJ. (1996). Environmental gradients across four rainforest - open forest boundaries in northeastern Queensland,. *Australian Journal of Ecology, 21*, 245-254.

Unwin, GL. (1986). Structure and composition of the abrupt rainforest boundary in the Herberton Highland, North Queensland *Australian Journal of Botany, 37*, 413-428.

VanDerWal, J, Shoo, LP, Johnson, CN, & Williams, SE. (2009). Abundance and the environmental niche: environmental suitability estimated from niche models predicts the upper limit of local abundance. *The American Naturalist, 174*(2), 589-594.

VanDerWal, J, Shoo, LP, & Williams, SE. (2009). New approaches to understanding late Quaternary climate fluctuations and refugial dynamics in Australian wet tropical rainforests. *Journal of Biogeography, 36*(2), 291-301.

Veblen, TT. (1982). Regeneration patterns in *Araucaria araucana* forests in Chile. *Journal of Biogeography, 9*(1), 11-28.

Veblen, TT. (1992). Regeneration dynamics In D. Glenn-Lewin, R. Peet & T. Veblen (Eds.), *Plant Succession: Theory and Prediction* (pp. 152-187). London: Chapman and Hall.

Veblen, TT, Burns, BR, Kitzberger, T, Lara, A, & Villalba, R. (1995). The ecology of the conifers of Southern South America In N. Enright & R. Hill (Eds.), *Ecology of the Southern Conifers* Melbourne Melbourne Univeristy Press

Veblen, TT, Schlegel, FM, & Escobar, B. (1980). Structure and dynamics of old-growth *Nothofagus* forests in the Valdivian Andes, Chile. *Journal of Ecology, 68*(1), 1-31.

Veblen, TT, & Stewart, GH. (1982). On the conifer regeneration gap in New Zealand: the dynamics of *Libocedrus bidwillii* stands on South Island. *The Journal of Ecology, 70*(2), 413-436.

Warman, L, & Moles, AT. (2009). Alternative stable states in Australia's Wet Tropics: a theoretical framework for the field data and a field-case for the theory. *Landscape Ecology, 24*, 1-13.

Weiher, E, van der Werf, A, Thompson, K, Roderick, M, Eric Garnier, E, & Eriksson, O. (1999). Challenging Theophrastus: a common core list of plant traits for functional ecology. *Journal of Vegetation Science, 10*(5), 609-620.

Werren, G. (2001). Environmental Weeds of the Wet Tropics Bioregion: risk assessment and priority ranking Cairns Wet Tropics Management Authority

White, M. (1998). *The Greening of Gondwana* (3 ed.). Sydney: Kanagroo Press.

Wiersma, YF, Huettmann, F, & Drew, CA. (2011). Landscape modeling of species and their habitats: history uncertainty and complexity In C. Drew, Y. Wiersma & F. Huettmann (Eds.), *Predictive Species and Habitat Modeling in Landscape Ecology* (pp. 1-6). New York Springer.

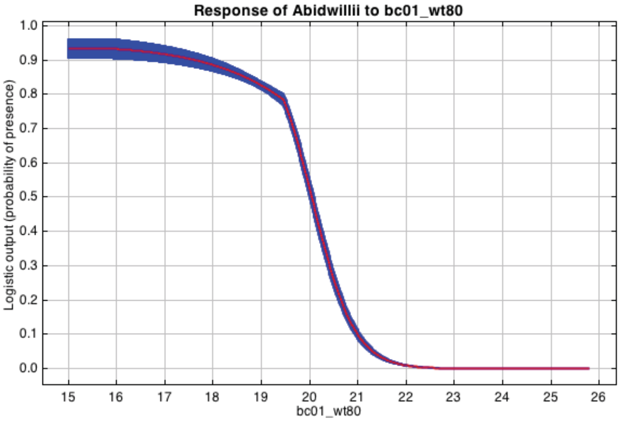
Womersley, JS. (1958). *The Araucaria forests of New Guinea - a unique vegetation type*. Paper presented at the Symposium on Humid Tropics Vegetation, Tjiawi, Indonesia.

Wood, S. (2014). Mixed GAM Computation Vehicle with GCV/AIC/REML smoothness estimation (Version 1.8-4).

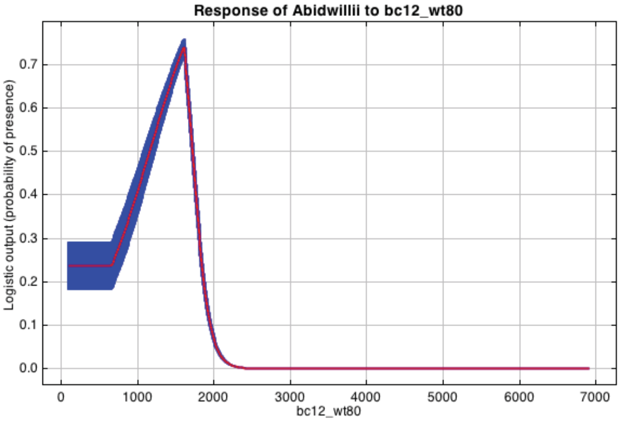
Xu, T, & Hutchinson, M. (undated). ANUCLIM Version 6.1 User Guide. Fenner School of Environment and Society The Australian National University

Zimmermann, NE, Edwards Jr., TC, Graham, CH, Pearman, PB, & Svenning, J-C. (2010). New trends in species distribution modelling *Ecography, 33*, 985-989.

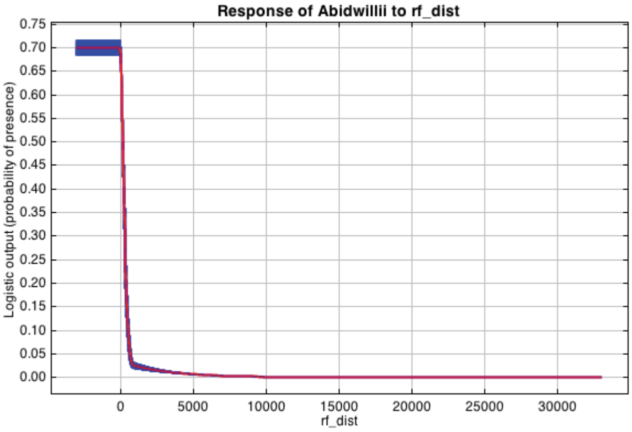
APPENDIX 1. Response Curves for Predictors



Mean annual temperature (C°).



Annual precipitation (mm).



Distance to rainforest (m).

APPENDIX 2. Leichardt Creek site characteristics.

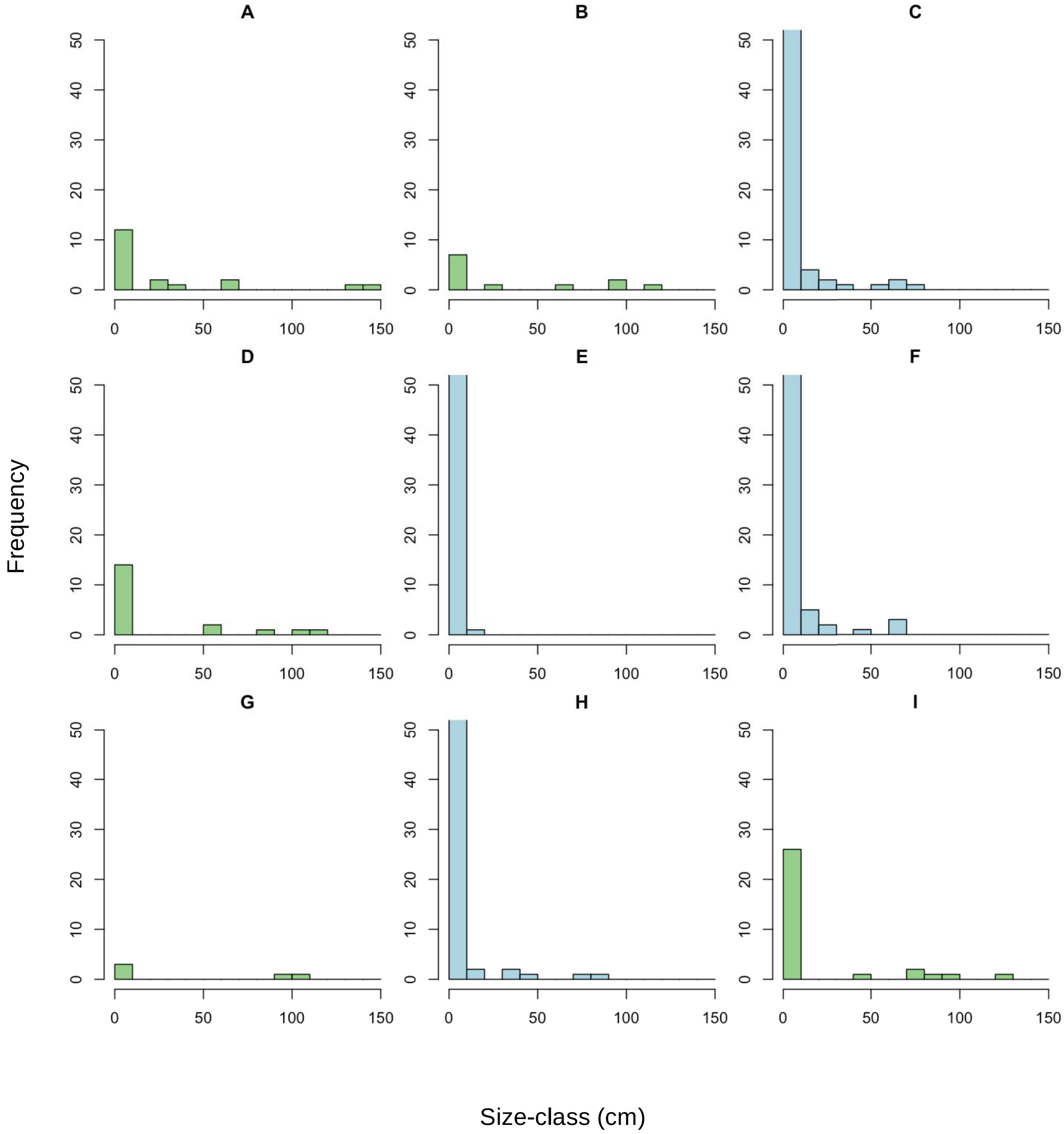
The following table summarises the characteristics of each sampling site in Chapter 3.

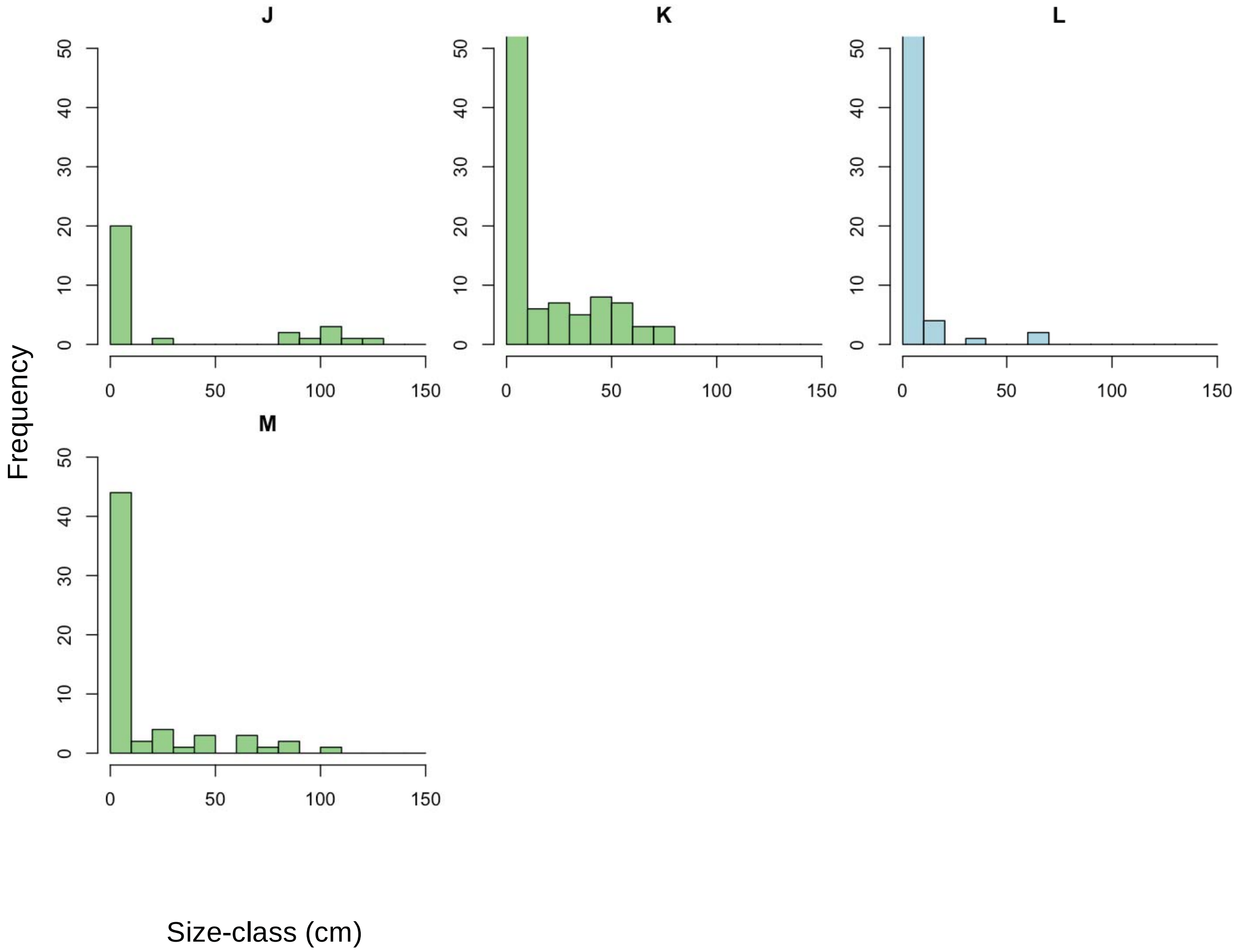
Site	Coordinates	Habitat Description	Area (ha)
A	-16.589176° 145.262850°	**Alt**: 858m. **Aspect**: south **BVG**: Rainforest Well-developed open understorey with numerous well-spaced large old trees indicative of negligible human disturbance. Species observed include *A. bidwillii*, *Podocarpus grayae*, *Argyrodendron peralatum*, *Elaeocarpus bancroftii*, *Flindersia* sp. and *Ficus* sp.. Understorey species include: *Calamus* sp., *Alpinia modesta*, *Alpinia hylandii* and other species.	0.64
B	-16.593271° 145.267912°	**Alt**: 895m. **Aspect**: north-west **BVG:** Rainforest Dense with an uneven canopy and thick understory. Canopy trees include several *A. bidwillii*, *Flindersia* sp., *Elaeocarpus* sp. and other Myrtaceae and Sapindaceae species. Understorey includes *Alpinia* spp., *Calanthe triplicata*, *Cordyline* sp., *Calamus* spp., and an abundance of ferns.	0.64
C	-16.589670° 145.259397°	**Alt**: 860m. **Aspect**: south-west **BVG:** Tall Open Forest *Eucalyptus grandis* is represented by few large old trees interspersed with *Syncarpia glomulifera* subsp. *glomulifera*, *Allocasuarina torulosa*, *Banksia aquilonia* with *A. bidwillii* present as reproductively mature adults, poles, saplings and seedlings together with an understorey including *Polyscias australiana*, various Myrtaceae, *Alyxia ruscifolia* and *Dendrocnide moroides*.	0.64
D	-16.589750° 145.257889°	**Alt:** 825m. **Aspect**: south **BVG:** Rainforest **A** steep sided gully with mature *A. bidwillii* dominating canopy together with a range of broadleaved angiosperms including various Cunoniaceae, Myrtaceae, numerous vines and understory species including *Alpinia* spp., *Dendrocnide moroides* and *Calamus* spp.	0.64
E	-16.591635° 145.260034°	**Alt:** 818m**. Aspect**: south **BVG**: Tall Open Forest Canopy dominated by *S. glomulifera* subsp. *glomulifera*, *E. grandis* interspersed with *Allocasuarina torulosa* and *A. bidwillii* with an understory supporting juvenile *A. bidwillii*, *Polyscias australiana*, various Myrtaceae, *Alyxia ruscifolia* and *Dendrocnide moroides* similar to Site C.	0.64
F	-16.591471° 145.261853°	**Alt:** 792m **Aspect**: west **BVG:** Tall Open Forest This site is characterised by an emergent and dominant canopy of *A. bidwillii* in an areas subject to inundation of fast flowing water from Leichhardt Creek. Other species present include *Schefflera actinophylla*, *Aceratium ferrugineum* together with numerous Orchidaceae, ferns and *Myrmecodia beccarii* as either epiphytes or lithophytes.	0.069
G	-16.590183° 145.264388°	**Alt:** 816m **Aspect**: south **BVG:** Rainforest Open understorey with several large old trees. Species observed include *A. bidwillii*, *Podocarpus grayae*, *Argyrodendron peralatum*, *Elaeocarpus bancroftii*, *Franciscodendron laurifolium*, *Garcinia warrenii*, *Syzygium* sp., and *Placospermum coriacium*. Understorey species include: *Calamus* sp., *Alpinia modesta*, *Alpinia hylandii* and other species.	0.64
H	-16.593071° 145.260092°	**Alt:** 719m. **Aspect**: north-west **BVG:** Tall Open Forest A complex site with late mature open forest with senescent *E. grandis*, mature *S. glomulifera* subsp. *glomulifera* and *A. bidwillii. Calamus* spp. are abundant and *Ficus* spp. occur in open forest canopy species. The palm *Oraniopsis appendiculata* is also present. *Dendrocnide moroides*, *Smilax australis* and *Alpinia* spp. are abundant.	0.64

I	-16.590024° 145.266533°	**Alt**: 951m **Aspect**: west **BVG:** Rainforest This site is partly dominated by some very large *A. bidwillii* and a range of broadleaved angiosperms including *Argyrodendron peralatum*, *Elaeocarpus bancroftii*, *Flindersia* spp., *Franciscodendron laurifolium, Syzygium* sp., and *Placospermum coriacium*. Understorey includes *Aglaia tomentosa, Alpinia* spp., *Ardisia brevipedata, Calanthe triplicata*, and *Calamus* spp.. Ferns are also abundant.	0.64
J	-16.591214° 145.264984°	**Alt**: 792m **Aspect**: north **BVG:** Rainforest **W**ell-developed with emergent *A. bidwillii* up to 50m. *A. peralatum, Franciscodendron laurifolium, Garcinia warrenii, Syzygium* spp.. *Calamus* spp. and *Pandanus monticola* dominate the understorey.	0.72
K	-16.591239° 145.262528°	**Alt**: 778m **Aspect**: north-west **BVG:** Rainforest (rocky) A dense stand of *A. bidwillii* beside Leichhardt Creek on exposed rocks with a shared canopy of *E. grandis* to the southern end and rainforest on the northern end with *Alyxia ruscifolia, Timonus singularis, Calanthe triplicata* in the understorey. *Acacia* sp., *Davidsonia pruriens, Darlingia darlingiana* are also present.	0.48
L	-16.592508° 145.260914°	**Alt**: 719m **Aspect**: north-west **BVG:** Tall Open Forest Characterised by mature and senescent *E. grandis* with a mixed understorey of open and rainforest species including *Allocasiuarina torulosa and Syncarpia glomulifera* subsp. *glomulifera.* This site also supports mature *Agathis robusta, Podocarpus graye* and *Ficus* sp. Understorey included *Calamus* spp., *Dendrocnide moroides* and the introduced *Lantana camara.*	0.48
M	-16.590575° 145.266315°	**Alt**: 949m **Aspect**: south-west **BVG:** Rainforest (rocky) *A. bidwillii* dominant species of mixed size/age classes. Open canopy with various understory species including *Timonus singularis, Alyxia ruscifolia, Calanthe triplicata, Freycinetia excelsa* and numerous epiphytes.	0.4

APPENDIX 3. Size-class frequency histograms for sites.

Leichhardt Creek size-class frequency distributions of *A. bidwillii* for each site. Rainforest sites are light green and tall open forest sites are light blue. For site descriptions see Appendix 2.




J
K
L
M
Frequency
Size-class (cm)
0
10
20
30
40
50
0
50
100
150